

Future impacts of climate change induced weather patterns on honey bee (*Apis mellifera*) foraging flight conditions in the Netherlands

Alexandra Drozdowska

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Supervised by: Dr. Ir. Arnold van Vliet
Examiner: Prof. Rik Leemans
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Environmental Systems Analysis Group



Dedication

This thesis is dedicated to my family; you encourage me to become a better scientist every day. It is also dedicated to the indomitable spirit of those who first figured out how to harvest honey; your perseverance paid off.

Acknowledgments

I would like to thank the various individuals who first helped plant the idea of doing a Masters in my head, and those who supported me during the thesis-writing process. I would also like to thank the volunteers at Hivetool.net and the Center for Honey Bee Research, specifically Paul for his enthusiasm and Steven Wynn for compiling and sending the vast amount of raw data.

Summary

The honey bee (*Apis mellifera*) is an essential contributor to global commercial agricultural outputs. It pollinates flowers while collecting nectar during foraging trips from the hive. The worldwide phenomenon ‘Colony Collapse Disorder’ has led to unprecedented colony losses. Honey bees are also potentially affected by climate change, since weather strongly affects honey bee foraging. However, the effect of current and projected future climate change on honey bees is poorly known. This study aims to determine the future impacts of climate-change induced weather patterns on honey bee foraging flight conditions and pollination potential in the Netherlands.

A literature review helped to determine the known environmental conditions conducive for honey bee flight for pollination/honey producing purposes revealed that honey bees are influenced by temperature, relative humidity, pressure, solar radiation, precipitation, wind speed, and light intensity. The ranges of these weather conditions in which honey bees forage vary due to their ability to compensate sub-optimal conditions in one weather factor with optimal conditions in another.

To determine whether the environmental conditions that were found in literature correlated with field data from Hivetool.org, three years of five-minute interval hive weight measurements by automated electronic hive scales and simultaneous weather conditions were analysed. The field site was located in Athens, Georgia, USA. Two datasets were created from the original dataset, with data sorted by their change in hive weight ($\geq -1\text{kg}$ to $<0\text{kg}$, 0kg , or $>0\text{kg}$ to $\leq 1\text{kg}$) or sorted by their weight class ($<44\text{kg}$, $\geq 44\text{kg}$ to $\leq 46\text{kg}$, and $>46\text{kg}$). The hive weight classes are considered to represent a hive in danger of starving, surviving, and thriving (respectively). The non-parametric Kendall Tau (τ) test revealed a more strongly related hive weight and weather than change in hive weight and weather (τ is 0.13 and τ is 0.04, respectively). Optimal flight conditions for foraging were determined by fractionating frequency counts of the $>46\text{kg}$ class. Daily optimal flight conditions were determined to have a mean temperature of 17 to 26°C ($\pm 1.0^\circ\text{C}$), a relative humidity of 70 to 90% ($\pm 5\%$), a solar radiation of more than 200 W·m² (± 25 W·m²), a precipitation of 5 to 25mm ($\pm 5\text{mm}$), a wind speed less than 10 km·h⁻¹ (± 2.0 km·h⁻¹), and a maximum wind gust less than 35 km·h⁻¹ (± 2.0 km·h⁻¹). These optimal flight conditions determined the exclusion criteria to create the Honey bee Optimal Flight Indicator (HOFI), which shows how many days within a dataset contain optimal conditions. The average amount of optimal flight days in the Netherlands was 15 days per year. When using only criteria found within the downloadable KNMI climate change scenarios (i.e. temperature, solar radiation, and precipitation) this number increased to 32 days per year. The KNMI scenarios are based on changes in global temperatures and air

circulation (small or large changes) and approximate climates around 2050 and 2085. In 2050 the amount of optimal flight days is projected to range between 39 and 46 days per year. By 2085 it should range between 39 to 50 days a year.

The current annual economic value of honey bees in the Netherlands is at least €1.1 and is based on the value per hectare of honey bee pollinated crop. Since the future number of flight days is expected to increase, the value should theoretically increase as well. Trends in the Dutch apiculture show subpar performance in comparison to other EU countries. This is likely due to lower hive density and fewer commercial beekeepers. Crop failures are expected to occur due to drought in the future. This puts increased pressure on farmers to ensure that their remaining crops are adequately pollinated to partially compensate their climate-change losses. This could increase demand for pollination services and would increase the economic value of honey bees. Therefore, as the number of optimal flight days for honey bees is expected to increase, the pollination service demand by farmers will be the main driver of the future economic value of honey bees.

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1 Intro

1.1 Honey bees as important pollinators

Pollination, which is an important ecosystem service, helps plants reproduce sexually (Klein et al., 2007). This is done by wind or animals (Ibid.). Animal pollination has been shown to increase the size, quality, and/or quantity of fruits, seeds and/or nuts (Ibid.). This service provided a global economic value of at least €153 billion in 2007 (van Engelsdorp & Meixner, 2010). In the EU25 the value is €14.2 billion and in the USA and Canada, €14.4 billion (Ibid.). Loss of animal pollinators would result in an 8% agricultural production loss, but this may be offset by increasing agricultural land by 15% in developed and 42% in developing countries, a solution unlikely to happen due to current land pressure (Ibid.). Examples of animal pollinators include a variety of insects (bees, beetles, and flies), birds, and bats (Ricketts et al., 2008), however the European or Western honey bee (*Apis mellifera*) is the most widely spread and used animal pollinator in the global agriculture sector (Van Engelsdorp & Meixner, 2010). The honey bee is a flying insect whose body consists of three main sections: the head where the mouth parts, antennae, and compound eyes are located; the thorax (middle) with the attached wings and legs; and the abdomen (end), which contains most organs and the stinger. The honey bee considered a social insect as it lives in a colony as opposed to being solitary. These colonies are matriarchal and contain only one reproducing insect (the queen) and her non-reproducing offspring. The vast majority of a colony is female while males (drones) are only present during the spring and early summer. Only females are considered workers, fulfilling a variety of tasks as they age such as being a nurse bee,

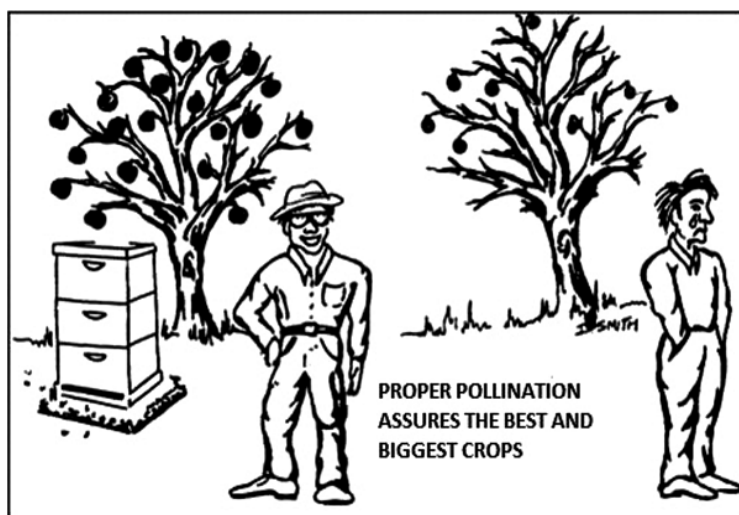


Figure 1 Educational material for farmers showing the benefits to crop production of having honey bees near plantations. Taken from Abrol, 2015.

fact that is promoted by governments around the world as a way to improve crop productivity (FIGURE 1). Even though only 35% of total agricultural output (by volume) is dependent on or improved by animal pollination, 75% of the top global crop species for human consumption are positively influenced by pollinators (Ibid.). The total land used for

undertaker, guard duty, before finally becoming a forager for nectar and pollen (Weiss & Vergara, 2002). While extracting the nectar, the hairs on the honey bee passively collect pollen, which is distributed to other flowers as it flies from flower to flower (Weiss & Vergara, 2002). In this way, the honey bee contributes about 80% of global animal pollination services (Lecocq et al., 2015), a

agriculture has increased since 1965 but the proportion of cropland not dependent on animal pollination has decreased (Van Engelsdorp & Meixner, 2010), likely due to pollinated crops having five times higher value (€151 vs. €761) (Gallai et al., 2009). This has resulted in an increased reliance on pollinators by 50% and 62% in developed and developing countries (respectively) between 1961 and 2006. One should note that the increase in agricultural land has been greater than the growth of the apiculture industry (300% vs. 45%, respectively) (Aizen & Harder, 2009), meaning that in the future, agricultural output is likely to be limited by the number of pollinators available (Van Engelsdorp & Meixner, 2010).

At least 28 subspecies of honey bees have been identified (Engel, 1999), but the following three are the most common in beekeeping (Weiss & Vergara, 2002):

- *Apis mellifera mellifera* - European dark honey bee/German black honey bee, brought over to the Americas by settlers from Europe (Weiss & Vergara, 2002)
- *Apis mellifera carnica* - Carniolan honey bee (Weiss & Vergara, 2002)
- *Apis mellifera ligustica* - Italian honey bee (Weiss & Vergara, 2002)

There are also different hybrids such as Buckfast and Africanized honey bee (a hybrid between *A. m. ligustica*, *A. m. scutellata* (African honey bee), and *A. m. iberiensis* (Spanish honey bee)).¹ Genetics affect flight speed, range, defensive response, some disease resistance (Abrol, 2012) and to some extent flight metabolic rates and thus foraging effort (Abrol 2006; Harrison & Fewell, 2002). For the purposes of this thesis, honey bee, western honey bee, and common honey bee all refer to the same species, *Apis mellifera*, henceforth referred to as honey bee. When a different species of bee is being discussed, it will be specified with the common name followed by its Latin classification.

1.2 Colony Collapse Disorder

At the time of writing, the public eye has been focused on the steady decline in honey bee colonies in North America and Europe since 2006 (Spivak et al., 2011), attributed to the phenomenon named Colony Collapse Disorder (CCD) where hives are seemingly abandoned despite still containing a queen, brood (bee larvae), honey, and pollen, with little to no traces of worker bees.² Colony losses often occur during the wintering period and in the USA have averaged at a high of 28.7% since 2006 but declined to 23.1% in 2013.³ There is difficulty in quantifying colony losses in Europe due to the non-standardized definition of CCD at the time of first occurrence (2007-2008) (Watanabe, 2008), coupled with weak monitoring

¹ http://apisenterprises.com/papers_html/Misc/AHB%20in%20the%20Americas.htm

² <https://www.epa.gov/pollinator-protection/colony-collapse-disorder>

³ <https://www.epa.gov/pollinator-protection/colony-collapse-disorder>

systems and a lack of both national and European Union scale data and collection methods (Hendrikx et al., 2009). The amount of colony losses attributed to CCD in the USA has decreased from 60% in 2008 to 31% in 2013, with no colony losses being attributed to CCD in initial reports for the 2014-2015 over-wintering period.⁴ A similar trend is observed in Europe with country losses ranging from 3.2% to 32.4% in 2012-2013, to 2.4% to 15.4% in 2013-2014, as reported in a pan-European epidemiological study (Laurent et al., 2016). However, the study noted a possible negative influence of a colder winter in 2012-2013 compared to a milder winter in 2013-2014 (Ibid.). Much research has been conducted on CCD (Spivak et al., 2011) and now researchers are generally in agreement that a combination of factors like the Varroa mite, viruses, management, insecticides, foraging conditions, and genetic diversity have contributed to recent global trend of honey bee declines (Van Engelsdorp & Meixner, 2010).

1.3 Climate change impact on bees

Another important trend that will likely affect honey bees is climate change. Climate is defined as the long term average (30 years) of weather conditions in an area, whereas weather is defined as their day-to-day variations.⁵ Since the climate is changing, it is indicative that weather has been changing as well. This is important as various studies have shown weather impacts honey bees. Weather influences:

- 1) hive entrance activity/flight activity (Szabo, 1980; Burrill & Dietz, 1981; Marceau et al., 1990; Danka et al., 2006; Vicens and Bosch, 2000; Corbet et al., 1993);
- 2) number of eggs laid (Pârvu et al., 2013);
- 3) honey yield (Holmes, W., 2002);
- 4) larvae feeding (Reissberger & Crailsheim, 1997; Schmickl & Crailsheim, 2002);
- 5) swarming (Pârvu et al., 2013);
- 6) foragers at a flower patch (Abrol, 2006; Corbet et al., 1993; Puškadija et al., 2007; Vicens and Bosch, 2000);
- 7) defence behaviour (Southwick & Moritz, 1987);
- 8) length of foraging (Xu-Jiang et al., 2016).

Many of these studies might not have found the real relation between weather conditions and bees as they involve short-term study periods ranging from a few days to three months. Furthermore, a majority of the studies involved active disturbance of the hive to obtain data. These disturbances to the hive can cause stress and cause honey bees to react differently than normal.

⁴ <https://www.epa.gov/pollinator-protection/colony-collapse-disorder>

⁵ http://www.nasa.gov/mission_pages/noaa-n/climate/climate_weather.html

Despite the limitations of these studies, substantial changes in weather and climate are likely to impact bees. The global temperature continues to rise⁶ and the 2014 report from the Intergovernmental Panel on Climate Change (IPCC) states the occurrence of heat waves is very likely to be more frequent and last longer, and precipitation extremes are likely to be more frequent and intense (IPCC, 2014). Also in the Netherlands climate will change in the coming decades. The Royal Netherlands Meteorological Institute (KNMI - Koninklijk Nederlands Meteorologisch Instituut) is a well-respected governmental organization that monitors and conducts research on, among others, weather and climate, and has contributed data to the IPCC reports.⁷ In 2006 the KNMI created scenarios to help various levels of government, organizations, and citizens understand what the effects of climate change are likely to look like in the Netherlands (KNMI, 2014). The scenarios were updated in 2014 based on the feedback of the initial scenarios and input from stakeholders (Ibid.). This data is available online where users may also upload their own climate data and transform them according to the KNMI scenarios (Ibid.).

Since honey bees are known to be strongly influenced by environmental conditions (Polatto et al., 2014), how will the projected changes in climate impact honey bees and specifically their foraging behaviour, on which our agricultural system depends on? When I first thought of this topic (which came to me in a dream), I was initially concerned about a mismatch occurring between flowering times and honey bee activity (a phenological mismatch), and how sensitive the apiculture industry is to climate change. Since the literature currently (2016) finds no phenological mismatch between pollinators and plants (Forest, 2014), I wanted to know if climate change would influence honey bee foraging days due to heat stress or changes in precipitation patterns (Ibid.) and if this would translate to the Netherlands becoming economically unfavourable for commercial beekeepers. There have been some studies done on predicting changes in honey bee pollination service in regard to temperature changes (Rader et al., 2013) as well as predicting honey yields in regard to temperature and precipitation changes (Delgado et al., 2012), but the former has a small sample size and the methodology of the latter cannot be easily applied to other areas. Furthermore, temperature, or temperature and precipitation, are not the only factors influencing honey bee foraging (Vicens and Bosch, 2000; Pârvu et al., 2013; Polatto et al., 2014). The flight behaviour of small bee species is more dependent on weather conditions, while for larger bee species it is nectar content (Weiss & Vergara, 2002). *Apis mellifera* being a medium sized bee in comparison to other *Apis* species (Weiss & Vergara, 2002), is therefore influenced both by weather factors and the volume and concentration of nectar (floral reward) (Willmer & Stone,

⁶ <http://climate.nasa.gov/vital-signs/global-temperature/>

⁷ <http://www.knmi.nl/over-het-knmi/about>

2004). However, the presence of predators or dead bees on or nearby nectar sources has been shown to decrease foraging visits (55% - 79%) and decrease time spent per flower (17 % - 33%) to those locations (Tan et al., 2013), with foragers preferring 'safe' nectar sources, though riskier behaviour is observed in honey-depleted colonies (Willmer & Stone, 2004). In inclement weather a similar trend is shown as a larger proportion of foragers from smaller colonies will forage when compared to that of a larger colony (Abrol, 2015). Thus in strong colonies, there likely to not be as large an increase in hive weight even if flight conditions for foraging are optimal if predators are present.

1.4 New bee monitoring data: Electronic hive scales

To determine the impact of changes in weather and climate on bee foraging next to all the potential factors requires detailed bee observations. The advancement of technology has now allowed beekeepers and scientists to wirelessly monitor hives through the use of electronic hive scales with sensor attachments (Meikle et al., 2008). Data such as hive weight, temperature, and humidity can be collected and uploaded to a database, in conjunction with other hives, to form beehive monitoring networks (Ibid.). Such networks have been set up in the United States of America (hivetool.net)⁸, Germany (Bienenkunde), Switzerland (Verein deutschschweizerischer und rätoromanischer Bienenfreunde) and Denmark (Nordic/Baltic honey meter) (Meikle & Holst, 2015; Human et al., 2013). The electronic hive scales allow beekeepers to monitor the nectar flow and colony health without disturbing the hive while giving researchers ample data to study the influence of the environment on honey bees (Meikle et al., 2008). Most of these networks record the hive weight and change in weight, coupled with the temperature and relative humidity in the hive, near the hive, or at a weather station nearby. Since the link between weather and foraging conditions is well established (Lundie, 1925; Burrill & Dietz, 1981; Meikle & Holst, 2015; Abrol, 2006), clear trends should be seen when using large datasets from hive monitoring networks to determine to what extent do the known environmental conditions conducive for honey bee flight for pollination purposes correlate with field data. However, these analyses have not been carried out so far.

1.5 Objective and research questions

The main objective of this study is to determine the impact of future climate-change induced weather patterns on honey bee (*Apis mellifera*) foraging flight conditions and pollination potential in the Netherlands.

To achieve this objective, I formulated the following Research Questions:

⁸ <http://hivetool.net/about>

1. What are the known environmental conditions conducive for honey bee flight for pollination purposes?
 - a. To what extent do the known weather conditions conducive for honey bee flight for pollination purposes correlate to hive weight or change in hive weight?
 - b. What are the optimal weather conditions conducive for honey bee flight for pollination purposes based on field data?
2. What is the current number of days with favourable honey bee flight conditions for pollination in the Netherlands?
3. What is the number of days with favourable honey bee flight conditions for pollination in the Netherlands under the different future climate change scenarios as used by KNMI?
4. What is the current economic importance of, and the trend of economic importance in the Dutch apiculture industry?
5. Is there a change in days with favourable honey bee flight conditions for pollination under the different climate change scenarios, as used by KNMI, and will it impact the pollination potential and pollination value in the Netherlands?

I structured this paper so that each chapter focuses on one aspect of each research question i.e. method, results, and discussion. By doing so, it allows for the reader to quickly browse which section is relevant to them and minimizes repetition. In the conclusions I will show how the results of this thesis are relevant for Dutch beekeepers and government.

2 Methods

This chapter presents the various methods used to answer the research questions. First background information was gathered through a literature search for research question 1a, whose results were used to determine the correlation in 1b, which was used to focus the method for data analysis in 1c, which became the foundation for the method for question 2 and 3. Another literature search was conducted for question 4, whose results were combined with formulating the method for question 3 to have input to finally answer question 5, allowing for the main question to be solved.

2.1 Literature study

The scientific literature was reviewed to determine the known weather factors that influence honey bee foraging flight. Since the honey bee is one of the best studied animals in the world, this results in many different studies (Capinera, 2008). The search was performed physically in the Wageningen University library and online using Global Search - Wageningen library's search engine, Google Scholar, Web of Science, and the USDA Project database using a combination of keywords: *Apis mellifera* climate change, bee climate change precipitation, honey bee environmental flight conditions, honey bee meteorological flight, honey bee weather, honey bee precipitation, honey bee wind, honey bee flight conditions, bee climate stress, *Apis* climate stress, and environmental stress in bees. References were carefully examined and cross-referenced to determine if the information was specifically for *Apis mellifera* or other bee species. The literature search was expanded to include why these factors influence honey bees to gain a better understanding of the potential impact of a combination of changes in various weather factors, as well as if there was a significant difference between bee sub-species as this information would influence how honey bees would respond to weather changes.

Having identified the weather factors influencing honey bee flight and the ranges of these weather factors when flight occurs, I determined if there is overlap with field data obtained from a honey bee monitoring network.

2.2 Analysing hive weight and weight change

Hive weight was chosen as an indicator for honey bee flight activity. The choice to use hive weight was based on studies by Marceau et al. (1990) and Szabo (1980). Marceau et al. found a strong relation ($r^2 = 0.79$) between honey bee flight activity and hive weight (honey production). A similar relationship was found by Szabo (1980) ($r^2 = 0.766$ to 0.879). In this study any hive weight gain as a result of foraging, larval growth, adult bees, or propolis and wax production was attributed to positive foraging conditions due to the law of conservation of mass. That is, hive weight gain was a result of foraging since it takes energy to produce wax, grow eggs into bees, and to maintain a population of bees (metabolic demand).

Therefore, a weight gain or no change in weight indicated that enough foraging occurred to cover the metabolic demand of the colony. Weight loss indicated weather conditions in which bees could not completely compensate for the metabolic demand of the colony (they may or may not have been able to leave the hive to forage).⁹ In these situations, the bees would have had to rely on their honey stores for energy. Meikle et al. (2008) found that on average 76% of hive weight can be attributed to food stores (honey or pollen), which, apart from supplementary feeding, comes directly from foraging. Therefore, the majority of the hive's weight always consists of honey, and the amount of honey is directly dependent on foraging, so a change in foraging conditions will result in a change in stored honey, which will be reflected in the weight. Although foraging/flight activity strongly determines the changes in hive weight, literature does show that humidity, precipitation, and wind have an influence on hive weight (Meikle et al., 2006; Stalidzans & Berzonis, 2013).¹⁰ Meikle et al. (2006) found that an empty hive can fluctuate about 100g over the course of a day and that a change of 400g was observed during a rain event. These findings are supported both by Dr. Wayne Esaias, a NASA research scientist, and Paul, my contact at HiveTool (personal communications, 2016). I assume, therefore, that the influence of precipitation and wind on the weight of the hive will be seen as an increase in weight during weather conditions in which honey bees are expected to not replenish the amount of honey consumed by the hive's metabolic demand, based on literature.

The choice to use the change in hive weight was based on the assumption that change in hive weight would show clearer thresholds than when using hive weight. A hive may have a weight of 50kg in March at the start of the nectar flow (the hive starts to gain weight) as well as in November, when the hive is losing weight; the weather may be quite different during these two periods but they would be grouped together since they are the same weight. However, using the short-term delta change would show weight gain or loss and by grouping the weather conditions when such gains or losses occur, a clearer signal should be visible. The choice to use the hive weight was based on the assumption that the hive weight could be more reliable than the change in hive weight, which, having a narrower range was more sensitive to wind, precipitation, and humidity changes.

The data from the HiveTool monitoring network was selected as their data was in English, recorded the same weather conditions used in KNMI future climate scenarios (which would aid analysis in **SECTION 3.5**), and the organizers were enthusiastic and supportive of this thesis topic when contacted.

⁹ <http://honey.beenet.gsfc.nasa.gov/Docs/ScaleHiveProtocol.pdf>

¹⁰ <http://honey.beenet.gsfc.nasa.gov/Docs/ScaleHiveProtocol.pdf>

Hive data was received for a hive in Athens, Georgia, USA. This hive was chosen because it was most familiar to Paul, my contact in this organization, and so he would be able to answer any arising questions about the colony. Another reason for selecting this dataset was the fact that it was the longest continued monitoring series available. Even though this hive is located in a warmer climate compared to the Netherlands, almost all honey bees in North America are descendants of the European honey bees brought over by European settlers, and European queens are commonly imported into the United States of America, so the genetic makeup is similar (Sheppard, 2012). The queen from the Athens hive was captured from a local wild swarm and is assumed to be an Italian/Carniolan mix (personal communications, 2016)

The dataset from August 19, 2013, to March 6, 2016, consisted of five-minute intervals of hive weight and weather conditions: temperature, relative humidity, wind, wind gust, pressure, solar radiation; and precipitation which was given in the daily cumulative amount. Hive weight was logged on site and sent wirelessly to the database where it was paired with weather conditions at that same moment (apart from precipitation, which was the cumulative hourly or daily value) from a weather station approximately 1.5km from the hive location. Since precipitation was given as the daily cumulative, it was omitted from this analysis since its impact on the hive weight or change in hive weight cannot be determined at the five-minute scale. Prior to analysis, data was imported into Microsoft Excel (2013) and cleaned up in sequential order by:

- Determining delta hive weight change between consecutive five-minute intervals
- Converting to the appropriate metric units based off of the United States customary units. *The original file contained headings for both systems of measurement but did not always contain metric values.*
- Removing assumed glitches in electronic software (hive weights of 0kg and 453kg)
- Removing hive weights less than 20kg (expected hive weights are 27kg to 136kg¹¹). *Less than 20kg was chosen as the exclusion criteria as some points between 20kg and 30kg followed a smooth decreasing or increasing pattern with no sudden jump indicating these were real data points.*
- Excluding delta hive weight changes greater than $\pm 1\text{kg}$ due to being unrealistic. Meikle et al. (2006) found hourly weight changes to be within 100g.
- Removing weights with temperatures below 5°C and solar radiation of $100\text{ W}\cdot\text{m}^{-2}$, based on lowest known temperature (Harrison & Fewell, 2002) and solar radiation

¹¹ <http://honey.beenet.gsfc.nasa.gov/Docs/ScaleHiveProtocol.pdf>

(Abrol, 2006) at which honey bees have been seen foraging and the fact that honey bees do not forage at night (Burrill & Dietz, 1981)

- Removing weights without complete data for all weather factors (e.g. Null, #Value!)
- Points were manually removed that showed a sudden unsustained decrease (**FIGURE 2**). *Unsustained is defined as when the hive weight increased by nearly 10kg after 10–15 minutes.*

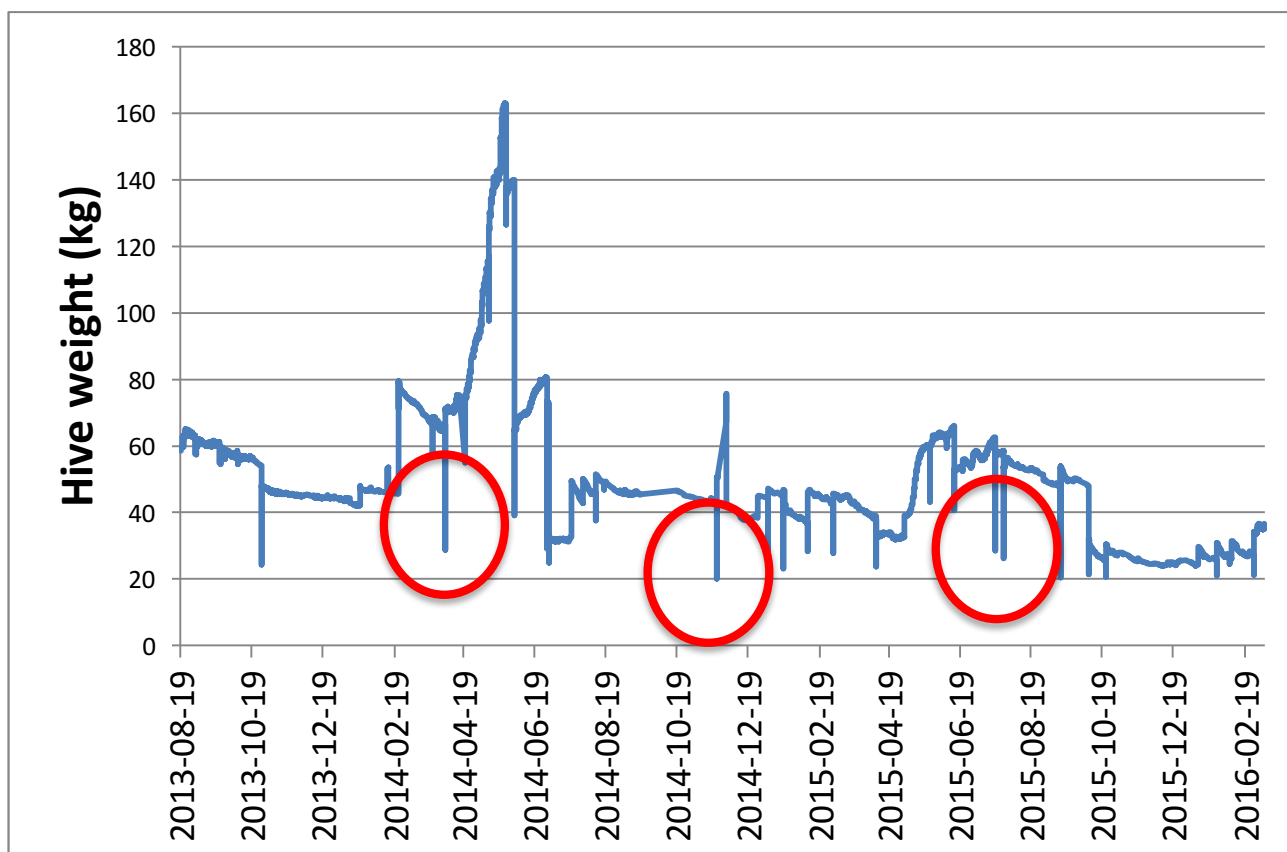


Figure 2 Hive weight over time with sudden temporary decreases highlighted (red circles)

This resulted in 68,981 usable observations from the original 240,407. This dataset was named 2013-2016. As temperature and humidity are likely closer linked to the metabolic demand of the hive (Szabo, 1980), while wind and rain are likely to have a stronger impact on foragers outside of the hive, delta hive weights were paired with the prior half hour average of weather conditions i.e. the change in hive weight at 08:00 would be paired with the average of weather conditions from 07:30, 07:35, 07:40, 07:45, 07:50, and 07:55. Data points that could not be paired with the prior half hour weather conditions due to gaps larger than 7.5 minutes between sampling times were removed. This resulted in 67,385 observations. This data set was named Paired 2013-2016.

Each weather variable was graphed over the full time scale and visually inspected for descriptive analysis. A sudden decrease and notable absence of wind and wind gust readings

from December 19, 2014, onwards were noted. Thus wind and wind gust analysis was not done using data after to December 19, 2014. This resulted in data sets 2013-2014 (37,876 observations) and Paired 2013-2014 (37,226 observations) being created.

It was noted that after (and including) November 30, 2014, hive and change in hive weight were recorded with two decimal points. In case this increase in accuracy influenced results, the databases 2015++ (32,305 observations) and Paired 2015++ (31,352 observations) were created using only data from November 30, 2014, onwards.

SPSS was used to test the hypothesis (Ho) that hive weight change and hive weight were not normally distributed. This was done using the Kolmogorov-Smirnov test of normality with Lilliefors Significance Correction to fulfil the criteria for statistical testing analysis. Non-parametric correlation using Kendall's Tau (τ) (Croux & Dehon, 2010) was run in SPSS in the event that datasets were not normally distributed. Kendall's Tau was used as it does not assume a linear relationship between dependent and independent variables and is considered less prone to error than Spearman's Ranked Correlation (Ibid.).

2.3 Determining optimal weather conditions

For each of the six datasets, hive weight change and hive weight were sorted into the weight classes negative ($\geq -1.00\text{kg}$ to $< 0.00\text{kg}$), zero (0.00kg), and positive ($> 0.00\text{kg}$ to $\leq 1.00\text{kg}$) and the weight groups ($< 44\text{kg}$), ($\geq 44\text{kg}$ to $\leq 46\text{kg}$), and ($> 46\text{kg}$) (respectively) along with their corresponding weather factors. Data sorting was required due to no emerging pattern when raw data were graphed. The hive weight groups are based on 45kg being a threshold where beekeepers would consider supplementary feeding to strengthen the hive.¹² The middle range ($\geq 44\text{kg}$ to $\leq 46\text{kg}$) is assumed to be equivalent to zero net weight change, indicating the colony being able to maintain their energy needs but not particularly thriving.

To determine the proportion under which weather condition values changes in hive weight or hive weight groupings occur, frequency tables were created of the sorted weather factors. The counts for each weather factor per range series or bin were summed and divided by the total sum of all the counts in that bin for either the hive weight change or hive weight groupings. The difference between subsequent bin fractions of the positive or $> 46\text{kg}$ values was taken. If the difference was less than 0.001 it was considered a negative difference. If the difference was greater than 0.001, it was considered a positive difference. If three subsequent bin fractions had a positive difference or if a negative bin difference was preceded by two positive bin differences, followed by two positive bin differences, the first positive difference bin was selected as the optimal value or start value of the positive correlation between each weather

¹² <http://www.bushfarms.com/beesfaqs.htm>

factor and hive weight change or hive weight. When three subsequent bin differences were negative or if a positive bin difference was preceded by two negative bin differences and followed by two negative bin differences, the first negative bin was selected as the end point of the positive correlation.

An ad-hoc rule was created to lessen the chance of outliers from skewing the frequency tables. Bin ranges were truncated when the total counts for that bin were equal to or greater than one percent of the total data points. If the sum of the values in that bin were less than one percent of the total data points, the bin was rejected and the table was truncated to remove that bin. If however, the bin's data points sum contained less than one percent of the total data points but was located between two other bins and their data points sum were equal to or greater than one percent of the total data points, the bin was retained. The observations contained in the bins that were truncated were not removed for the other weather factors.

The one percent values for the different datasets were: 323 for 2015++, 314 for Paired 2015++, 690 for 2013-2016, 674 for Paired 2013-2016, 379 for 2013-2014, and 372 for Paired 2013-2014.

Having established what the optimal meteorological conditions are for honey bee foraging, I needed to determine how this translates into the current number of days with favourable honey bee flight conditions in the Netherlands. This was done by using the established meteorological conditions as criteria combined with the KNMI historical database.

2.4 Determining the current number of optimal honey bee flight days

Historical daily averages from De Bilt (relative humidity (%)) and De Kooy/Den Helder (wind and maximum wind gust (both $0.1 \text{ m}\cdot\text{s}^{-1}$)) from January 1, 1981, to December 31, 2010, were downloaded from the KNMI website.¹³ These stations and time period were chosen because they are used as the base reference for the KNMI climate scenarios (KNMI, 2014). The daily average temperature (0.1°C), global radiation ($\text{J}\cdot\text{cm}^{-2}$), and precipitation (0.1mm) were downloaded from the transformation page of KNMI. All of these components form the reference data upon which the KNMI scenarios are based on (KNMI, 2014). The scenarios, unfortunately, do not contain pressure (kPa), and so it was excluded from this analysis. Since the historic data is given in daily averages, the hive data had to be reprocessed to compare optimal values with historic data. Thus the original hive data was cleaned up using the same procedure as in **SECTION 2.2**, omitting the last step, the removal of temperature values below 5°C and solar radiation values lower than $100 \text{ W}\cdot\text{m}^{-2}$. This reprocessing only involved

¹³ <http://www.knmi.nl/nederland-nu/klimatologie/daggegevens>

hive weight since the correlation was discovered to be stronger (**SECTION 2.2**). The daily averages were calculated for the 2015++, 2013-2016, and 2013-2014 datasets. Paired datasets were excluded since averaging of the day would result in similar values with the non-paired datasets but would be less robust than the non-paired sets as data points had been removed during the pairing procedure. The daily average values and maximum daily wind gust were obtained from pivot tables, and these were grouped in the same manner as in **SECTION 2.3**.¹⁴ The optimal start values and or end values were determined using the same method as in **SECTION 2.3**.

The optimal daily average values for temperature (°C), relative humidity (%), solar radiation ($W \cdot m^{-2}$) and precipitation (mm) from the 2015++ dataset with wind ($km \cdot h^{-1}$) and maximum wind gust ($km \cdot h^{-1}$) from the 2013-2014 dataset were used in the creation of the Honey bee Optimal Flight Indicator (HOFI), which calculates how many days in a dataset meet all the criteria (optimal daily averages). The 2013-2016 dataset was omitted due to having an irregular gap in the optimal daily temperature value that was not found in the literature. A simplified HOFI was then created with only temperature (°C), solar radiation ($W \cdot m^{-2}$), and precipitation (mm), to be able to compare with the downloaded transformed climate scenarios data from KNMI in **SECTION 2.5**.

Some of the De Bilt historic values needed to be converted into the same units as the optimal daily values, with global radiation ($J \cdot cm^{-2}$) being the most difficult. This was due to no straight conversion being available to solar radiation ($W \cdot m^{-2}$). Conversion was done by assuming that since global radiation ($J \cdot cm^{-2}$) is given as a daily value, it can be written as $J \cdot cm^{-2} \cdot day$, and, assuming that each interval of solar radiation from the hive dataset was the value captured during one second, dividing by 86,400 seconds (24 hrs·60 min·60 sec) yielded **EQUATION 1**. For precipitation, values less than 0.05 mm were listed at -1 (0.1mm) in the historic dataset. This was changed to 0 to aid in analysis.

Equation 1 Converting $J \cdot cm^{-2}$ to $W \cdot m^{-2}$

$$\frac{J}{cm^2 \cdot day} \cdot \frac{10\,000}{86\,400} = \frac{W}{m^2}$$

Once the unit conversion was taken care of, the optimal daily values were used as exclusion criteria in MS Excel using the COUNTIFS function with the HOFI. The HOFI output was divided by 30 to determine an approximate average of optimal days per year over the 30-year period. A sensitivity analysis was done by determining the approximate average of optimal days per year when a different weather criterion was excluded from the HOFI. Instead of having six criteria, the HOFI was run using only five, and the number of days recorded when

¹⁴ (<44kg), (≥44kg to ≤46kg), and (>46kg)

one of the six criteria was excluded. A sensitivity analysis was carried out with the simplified HOFI; instead of having three criteria, it was run using only two, and the number of days recorded. This was done to identify the limiting factor(s) in the two HOFIs to be able to hypothesize what the impact of weather changes are likely to be in future climates. This will aid in comparisons in **SECTION 3.5** as only temperature, solar radiation, and precipitation are available in the transformed data series for scenarios. While only these three factors are downloadable for analysis, the four climate scenarios contain summaries for all six factors (temperature, relative humidity, wind, max wind gust, solar radiation, and precipitation) allowing us to estimate what the impact are likely to be.

2.5 Determining the future number of optimal flight days

Having established in **SECTION 2.3**, the reference point for the current amount of optimal honey bee flight days in the Netherlands using the HOFI, we may now move on to see how this number may change according to the climate scenarios of KNMI.

The reference data (January 1, 1981, to December 31, 2010) used to create the KNMI scenarios was based on the daily averages of temperature ($^{\circ}\text{C}$), relative humidity (%), and global radiation ($\text{J}\cdot\text{cm}^{-2}$) from De Bilt; wind ($0.1\text{ km}\cdot\text{h}^{-1}$) and maximum wind gust ($0.1\text{ km}\cdot\text{hr}^{-1}$) from De Kooy/Den Helder; and precipitation of homogenised values from 103 different weather stations in the Netherlands (KNMI, 2014). Average daily values for temperature ($^{\circ}\text{C}$), global radiation ($\text{J}\cdot\text{cm}^{-2}$), and precipitation (0.1mm) were downloaded for two different data sets, 2050 and 2085, with four scenarios (GL, GH, WL, WH) from the KNMI website.¹⁵

There are four scenarios grouped by two factors: the rise in global temperature (moderate –G [from the Dutch Gematigd, meaning moderate] – or warm – W) and change in air circulation (low – L – or high – H), which are the two most likely changes to occur in the Netherlands around the years 2050 and 2085 (since scenarios cannot predict exact dates), based off of the 2013 IPCC report. The scenarios incorporate natural climate variability based from 1951 – 1980 data and use the data from 1981 – 2010 as their transformation base. By incorporating natural variation into the scenarios, it gives a more realistic view of what weather is likely to be and can show how much ‘normal’ weather is affected over time (KNMI, 2014). More details about the scenarios, how they were constructed, and the data transformation process can be read in-depth in KNMI’14: Climate Change scenarios for the 21st Century – A Netherlands perspective (KNMI, 2014).

The simplified HOFI developed in **SECTION 2.4** (temperature, solar radiation and precipitation) was used to calculate the optimal flight days for each scenario and time period

¹⁵ http://www.klimaatsscenarios.nl/toekomstig_weer/transformatie/index.html

using the downloaded scenarios and time periods. A sensitivity analysis was conducted using the simplified HOFI like in **SECTION 2.4** to determine what the limiting factor(s) may be and if they are different from the reference period.

To determine if there is a significant difference between the number of optimal days in the reference period (1981-2010) and the number in each scenario and time period, MS Excel was used to test the null hypothesis (H_0) that the average number of optimal flight days (mean) from the reference data is the same in each scenario. First, an F-test was done to determine homoscedasticity, to determine the appropriate t-test for two-tailed variances. This test was also repeated for values with an excluded criterion (e.g. temperature and solar without precipitation).

2.6 Determining the economic value of honey bee pollination services

The economic valuation of pollination services by honeybees may be done by determining the price farmers pay to beekeepers for bringing enough colonies for adequate pollination (pollination market), or the cost associated with pollinating by hand (Eardley et al., 2006). This is a thesis project in and of itself so a literature search was done to approximate a value.

The literature search was done using Google Scholar and Wageningen Library with the key word combinations of Dutch honey bee pollination value and Netherlands honey bee pollination service. Statistics about Dutch beekeepers and honey/bee product sales were searched for on Statistics Netherlands (CBS), FAOStat (a division of the United Nations), and EuroStat (the agency responsible for statistics in the European Union). The economic value of pollination services in the Netherlands was assumed to consist of honey and other beekeeping product (wax, propolis, pollen) sales as well as any pollination market value.

2.7 Determining the future economic value of honey bee pollination

The current and future number of days with favourable honey bee flight conditions for pollination was taken from **TABLE 9** in **SECTION 3.5**. The assessment of the potential change in economic value of pollination under future scenarios was based on the cross-ratio of the current economic value of honey bees in the Netherlands (determined in **SECTION 3.6.1**) and current optimal days (**TABLE 9**), with the estimated optimal days for each time period and scenario (**TABLE 9**). This was synthesized with a literature search on the impacts of climate change in the Netherlands, beekeeping trends in the Netherlands, and basic socio-economic projections for the Netherlands to determine whether the pollination potential changes due to climate change in the future. The literature search was conducted using Google Scholar and terms used were a combination of climate change Netherlands, effects of, global warming, flood, Netherlands GDP projection, and food scarcity.

3 Results

Now the results of the methods mentioned in the previous chapter are presented. The results for each research question are grouped together in one section to facilitate the flow of thought through this thesis as they shape and build upon the subsequent research question.

3.1 Honey bees and weather

3.1.1 Factors influencing honey bee foraging flight

The following weather factors that influence honey bee foraging flight were identified: temperature, relative humidity, barometric pressure, solar radiation, precipitation, wind speed, and light intensity. The number of supporting studies for each factor is shown in **TABLE 1**.

3.1.2 Differences between colony size or bee subspecies

Danka et al. (2006) found larger colonies had a larger flight response rate to temperature changes while smaller colonies respond more to the time of the day, with more foragers leaving larger colonies at cooler temperatures compared to smaller colonies. Despite general claims that large differences occur between bee subspecies (Danka et al., 2006), little evidence could be gathered. Danka et al., (2006) found no direct difference between Russian (variety) and Italian (*A.m. ligustica*) colonies of the same size in response to temperature (Danka et al., 2006). Coroian et al. (2014) found that average temperature rather than geographic regions had a stronger impact on honey bee subspecies differentiation within the same geographical region, and Harrison & Fewell (2002) found that Africanized bees (*A.m. scutella* x cross) have significantly (10% - 20%) higher metabolic rates during flight compared to *A.m. ligustica* at the same temperature.

3.1.3 Ranges

The ranges of individual environmental factors are difficult to extract, but, a literature search is summed up in **TABLE 1**. Note that these values do vary between inter-colonies and are possibly be a result of genetic or local adaptation, but intra-colony ranges are much narrower (Harrison & Fewell, 2002). If possible, the study area used in the reference is provided.

Table 1 Summary of weather factor supporting references and ranges influencing honey bee foraging flight

Weather Variable	Supporting References	Commence Foraging	Peak Foraging	End Foraging
Temperature (°C)	19	5 (Harrison & Fewell, 2002) 6.57–10 (China) (Abou-shaara, 2014) 8.7–11.2 (Corbet et al., 1993) 9 (Burrill & Dietz, 1981; Crane, 1990) 11 (Corbet et al., 1995) 12 (Rohnstock, 2011) 12–14 (Vicens and Bosch, 2000) 10, 12–14 (spring) (Kevan & Baker, 1983) 13 (Abrol, 2015) 14–16 (May) (Kevan & Baker, 1983) 16 (India) (Abrol, 2006; Abou-shaara, 2014) 16–18 (summer) (Kevan & Baker, 1983)	20–28 (Puškadija et al., 2007) 38 (Kevan & Baker, 1983)	40 (Hepburn & Radloff, 2011) 42–48 (Kevan and Baker, 1983) 43 (Lithuania) (Abou-shaara, 2014) (Abrol, 2015) 43–46* (Crane, 1990) 45 (Harrison & Fewell, 2002)
Humidity (%)	7	75 (India) (Abrol, 2006)	40–50, 65–75 (Puškadija et al., 2007) 14.5–70 (Pârvu et al., 2013)	
Pressure	2	No information found	No information found	No information found
Solar Radiation (W·m ⁻²)	6	100 (India) (Abrol, 2006) 300 (Vicens & Bosch, 2000)	0.66 langley's\$ (Meikle & Holst, 2015)	
Precipitation (mm·day ⁻²)	3	No information found	1.0 (Rohnstock, 2011)	No information found
Wind Speed (km·h ⁻¹)	8	0 (assumed)	11 (Israel) (Kevan & Baker, 1983) 18 (Crane, 1990)	14 (Israel) (Kevan & Baker, 1983) 19 (California High Speed Rail Authority, 2012) 24–34 (Kevan & Baker, 1983)
Light Intensity (lux)	6	800 (India) (Abrol, 2006)	>500 (Kevan & Baker, 1983)	<10 (end of day)(Kevan & Baker, 1983)

* With ability to tongue lash

\$Lack of data for conversion to W·m⁻²

3.1.4 Causes of influence on honey bee flight

3.1.4.1 Temperature

Temperature appears to be the most referenced environmental factor influencing honey bee flight based on the amount of literature found **TABLE 1**, and the most influential (Holmes, 2002) if not limited by precipitation, solar radiation, or wind (Danka et al., 2006), though this is disputed by others (Abrol, 2015; Abrol & Kapil, 1986).

Insects are generally ectotherms; reliant on their environment for heat (Willmer & Stone, 2004). But the honey bee, while it is an insect, is also able to regulate to some extent its own body temperature, making it heterothermic (Willmer & Stone, 2004). Honey bees have twice the metabolic rate of flight muscles compared to hummingbirds and 30 times of human athletes (comparing the metabolic rate of base muscles) (Harrison & Fewell, 2002). As 10%–30% of a honey bee's energy supply is spent on flying with the remainder being converted into heat, it can use this heat to thermoregulate (Willmer & Stone, 2004). For the honey bee to be able to generate lift, its flight muscles, located in its thorax, must be an average of 35°C (Crane, 1990; Willmer & Stone, 2004), and while it is possible for the bee to shiver to warm up the muscles, it does not want to use too much energy doing so (Willmer & Stone, 2004). Esch (1976) found a linear positive relationship between wingbeat frequency and thorax temperature, with average lift more than doubling from 24°C to 33°C (Esch, 1976). This amount of lift remains constant between thorax temperatures of 33°C–38°C (Esch, 1976), supporting Crane's and Willmer & Stone's value of an average of 35°C. The difference between the ambient air temperature and thorax temperature in the late spring and early summer tends to be 10°C (Esch, 1976) so the thorax will achieve appropriate temperature during flight when the air temperature is less than 20°C–25°C, assuming minimal temperature to commence foraging occurs (Harrison & Fewell, 2002). Maximum lift is achieved in thorax temperatures above 40°C, and so will not occur at ambient temperatures under 30°C, but then will need to actively cool at ambient temperature above 36°C to prevent overheating the thorax (Esch, 1976) as a thorax temperature of 46°C is the upper limit for honey bees (Crane, 1990). In addition to this, pollen requires 10% more energy to transport than nectar, thus giving off more heat so in higher temperatures honey bees are less likely to collect pollen (Willmer & Stone, 2004).

The ambient temperature, energy reserves of the bee, and floral reward plays a large role in whether the honey bee will attempt to forage (Willmer & Stone, 2004). The possibility for thermoregulation gives the honey bee an advantage against non-thermoregulating pollinators since it allows them to start foraging earlier in the day (Willmer & Stone, 2004). A further advantage of *Apis mellifera* is that its hive is maintained at 34.5°C–35.5°C, making foragers

pre-warmed for flight resulting in farther distances travelled (Tan et al., 2012). The efficiency of foraging increases with temperature. Harrison & Fewell (2002) found that metabolic rate in the hive was three times higher in air temperatures of 20°C compared with 40°C. They propose that the accumulation of honey should triple as well since less energy is needed to maintain the hive (Harrison & Fewell, 2002). As mentioned, the honey bee can cool itself (Willmer & Stone, 2004), but this is discussed in the Humidity section next.

3.1.4.2 *Humidity*

Humidity is the amount of moisture or water vapour in the air.¹⁶ It influences whether the honey bee is capable of lowering its body temperature through tongue-lashing, which is when it places a drop of nectar onto its head, which evaporates and cools the bee (Willmer & Stone, 2004). This allows honey bees to survive high temperatures when humidity is low, but at risk of eventual dehydration if fluids are not replenished (Free & Spencer-Booth, 1962). When humidity is high this ability is compromised and thus honey bees will not attempt to forage (Pârvu et al., 2013) as this would cause the thorax to overheat (Polatto et al., 2014). Another influence of humidity on honey bees, though indirectly, is through nectar concentrations in flowers (Abrol, 2012). It was observed that when nectar became too concentrated, honey bees stopped visiting flowers but restarted as the nectar diluted (Ibid.). Conversely, too diluted nectar concentrations are not appealing to honey bees, but dry winds were shown to concentrate nectar to a level appealing to honey bees (Abrol, 2015). On hot dry days, honey bees prefer to forage at flowers with more dilute nectar, likely to gather nectar and cooling water at the same time (Abrol, 2006). The preferred nectar concentration is related to tongue length and the energy used to acquire the nectar vs. energy gained, as thicker nectar requires more effort to obtain and thinner nectar requires more energy to concentrate (Willmer & Stone, 2004).

3.1.4.3 *Barometric pressure*

No literature values could be found and only scant literature was found supporting the notion that barometric pressure influences honey bee flight behaviour (Lundie, 1925; Southwick & Moritz, 1987).

3.1.4.4 *Solar radiation and Light intensity*

These two factors have been grouped together as they are closely related: solar radiation refers to energy (predominantly ultraviolet, visible, and some infrared) from the sun that reaches earth¹⁷, while light intensity is how bright the visible light is perceived according to the human eye.¹⁸ Solar radiation may be called solar irradiance, given in Watts per metre

¹⁶ <https://climate.ncsu.edu/edu/k12/.humidity>

¹⁷ http://missionscience.nasa.gov/ems/13_radiationbudget.html

¹⁸ <http://www.giangrandi.ch/optics/lmcdcalc/lmcdcalc.shtml>

squared ($\text{W}\cdot\text{m}^{-2}$), while light intensity may be called illuminance, given in lux where one lux is equal to one lumen per metre squared ($\text{lx} = \text{lm}\cdot\text{m}^{-2}$).¹⁹ They appear to have different influences on honey bee foraging flight due to bee physiology.

Honey bees have three types of photoreceptors: green, blue, and ultraviolet (UV) (Kevan et al., 2001). This means that honey bees cannot see the colour red as humans see it, but instead view it as black (Backhaus, 1992a). Honey bees require colour contrast to differentiate between objects, meaning that there must be enough colour difference between the background and the object in order for the honey bee to accurately detect it (Kevan et al., 2001). Honey bees are also more sensitive to UV compared to green and blue frequencies, but this is usually not a problem due to low levels of UV rays in the atmosphere (Ibid.). However, studies have shown that increased UV rays reduce the contrast for honey bees making an object more difficult to find (Ibid.). Honey bees also do not respond to brightness (intensity) (Backhaus, 1992a) and instead rely on colour consistency, which is the ability to identify the same colour whether it is in the sun or shade; this enables the honey bee to quickly and accurately forage on the same plant species in the shade or intermittent sun (Kevan et al., 2001). Colour consistency is possible when groups of different photoreceptors overlap, as is the case with honey bees, with extensive overlap between green and blue receptors with UV receptors (Ibid.). The downside to this is what is known as the Bezold-Brücke Shift (Backhaus, 1992b), where colours appear to change based on the light intensity on the object; this makes blue objects seem green while red objects become more yellow.²⁰

There appears to be a negative quadratic influence of solar radiation on the number of foragers leaving the hive (Burrill & Dietz, 1981; Meikle & Holst, 2015). In other words, the number of foragers leaving the hive increases in relation to increasing solar radiation reaching a threshold and then decreases with increased solar radiation. This is likely due to honey bees using the infrared waves from solar radiation to increase their thorax temperatures for flight; once a threshold is reached, it would become too energy intensive to cool off the thorax and so foraging decreases (Willmer & Stone, 2004).

Honey bees will not leave the hive without adequate visible light, even if the ambient temperature is suitable for flight (Burrill & Dietz, 1981). This is likely due to poor visibility in low light, causing bees to fly slower which is more energy intensive (Willmer & Stone, 2004). However, honey bees start foraging at lower light intensities than when foraging is finished at the end of the day (Kevan & Baker, 1983) and it is believed this behaviour is predominantly a

¹⁹ <http://www.giangrandi.ch/optics/lmcdcalc/lmcdcalc.shtml>

²⁰ <http://eilv.cie.co.at/term/86>

cost-benefit analysis of a combination of decreases in light intensity and solar radiation (Hepburn & Radloff, 2011) with nectar reward (Danka et al., 2006).

Combining these facts, it can now be explained why solar radiation and light intensity have a negative quadratic influence honey bee foraging flight; solar radiation aids in the energy-efficiency of flight, while both solar radiation and light intensity are needed for the honey bee to see, but after a threshold, solar radiation and light intensity make it difficult for the honey bee to locate the target plant species, supporting Abrol's (2015) findings.

3.1.4.5 *Precipitation*

The common claim in the scientific and beekeeping literature is that “rain generally hampers” (Kevan & Baker, 1983, pg. 435) honey bee flight activity, and has been used to confine honey bees to their hives during experiments (Schmickl & Crailsheim, 2002). However, there have been very few studies to quantify why and to what extent precipitation influences honey bees. Xu-Jian et al. (2016) have observed that honey bees tend to make longer foraging trips and work longer on the day prior to a rainy day, perhaps to gather extra resources if the rain prevents foraging the next day. Joshi & Joshi (2010) observed that honey bees foraged within 100 m of their hive during rain showers, while a literature review by Rohnstock (2011) found that honey bee flight was restrained at $1 \text{ mm} \cdot \text{day}^{-1}$.

3.1.4.6 *Wind Speed*

How wind speed affects honey bee foraging flights is a matter of simple physics. The speed of a honey bee, at minimal thorax temperature for flight ($c.35^{\circ}\text{C}$) is around $11\text{--}12 \text{ km} \cdot \text{h}^{-1}$ (Esch, H., 1976). The average speed of a honey bee carrying nectar or pollen is $24 \text{ km} \cdot \text{h}^{-1}$, thus in wind speeds at or above this amount requires additional energy expenditure, and therefore they would prefer to forage at lower wind speeds (California High Speed Rail Authority, 2012). At wind speeds lower than this, bees are able to “make up” for a head wind by either flying faster to or from a nectar source by using the carrying force of the wind (Crane, 1990).

3.2 **Correlating hive weight or weight change with weather conditions**

Normality testing revealed that both hive weight change and hive weight had p-values of 0.000, therefore the null hypothesis that both data sets were not normally distributed was accepted. Various data transformations were attempted, namely Box-Cox and Spearman Ranked Correlation but these transformations were unsuccessful, and therefore regression analysis was not conducted. Results (**TABLE 2**) showed a higher correlation between hive weight and weather factors ($\tau = 0.13$) compared to hive weight change ($\tau = 0.04$) when the correlation from all six datasets was averaged. Between datasets, Paired 2015++ had the highest average difference of 0.18, while 2013-2014 and Paired 2013-2014 had the lowest with $\tau = 0.03$. Therefore, further analysis using hive weight change did not proceed.

Table 2 Correlations coefficients using Kendall's tau showing a higher correlation between hive weight and weather factors when compared with change in hive weight. Average correlations were calculated using absolute values.

Dataset	Weight Type	Temp (°C)	Relative humidity (%)	Pressure (kPa)	Solar radiation (W·m ⁻²)	Average correlation (τ)	Difference (τ)
2015++	Hive	0.24	0.11	-0.12	0.08	0.14	0.10
	Change	0.08	-0.05	-0.01	0.01	0.04	
Paired 2015++	Hive	0.45	0.09	-0.20	0.12	0.21	0.18
	Change	0.10	-0.03	-0.02	-0.01	0.04	
2013-2016	Hive	0.24	0.11	-0.12	0.08	0.14	0.10
	Change	0.08	-0.05	-0.01	0.01	0.04	
Paired 2013-2016	Hive	0.24	0.11	-0.12	0.08	0.14	0.10
	Change	0.08	-0.05	-0.01	0.01	0.04	
2013-2014	Hive	0.09	0.04	-0.10	0.08	0.08	0.03
	Change	0.06	-0.08	-0.02	0.04	0.05	
Paired 2013-2014	Hive	0.09	0.05	-0.09	0.09	0.08	0.03
	Change	0.06	-0.08	-0.03	0.05	0.05	

3.3 Optimal weather conditions for foraging

Clear signals were observed for all datasets and weather factors apart from the optimal start value for the pressure in Dataset 2015++. To aid in visualizing optimal start and endpoints, **FIGURE 3** demonstrates graphs constructed based on the fraction results for each weather factor using Paired 2015++ (as it had the highest correlation) with optimal start and end points circled. Optimal start and end points are summarized in **TABLE 3**, with the margins of error listed in the first column arising from the intervals between bins used to group data.

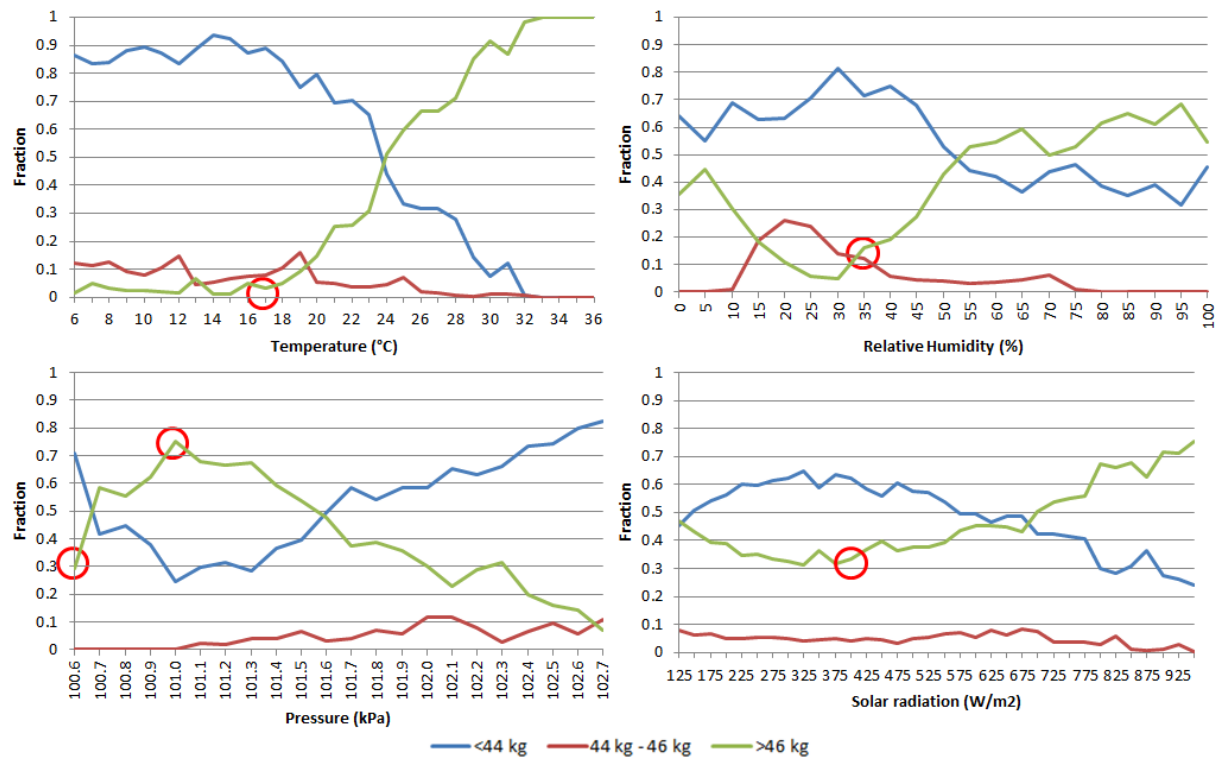


Figure 3 Optimal start and end points illustrated (with red circle) using fractions based on frequency counts for different weather factors using Paired 2015++ data.

Table 3 Summary of optimal start (and end) values for different datasets based on the fraction of frequency counts for different weather factors grouped into (<44kg), (≥44kg to ≤46kg), and (>46kg).

Weather Condition	Datasets					
	2015++	Paired 2015++	2013-2016	Paired 2013-2016	2013-2014	Paired 2013-2014
Temperature (±1.0°C)	12+	15+	12+	13-27	N/A	N/A
Relative Humidity (±5%)	30+	35+	30+	30+	N/A	N/A
Wind (±2.0 km·h ⁻¹)	N/A	N/A	N/A	N/A	≤12	<10
Wind Gust (±2.0 km·h ⁻¹)	N/A	N/A	N/A	N/A	≤26	10–22
Pressure (±0.1kPa)	100.6*–101.3	100.6–101.0	100.7–101.6	100.7–101.0	N/A	N/A
Solar Radiation (±25 W·m ²)	525+	400+	600+	325+	N/A	N/A

*clear start value not found – assumed based on including excluded criteria to estimate start value

3.4 Current number of optimal honey bee flight days

Optimal start and end points are summarized in **TABLE 4**, with the margins of error resulting from the intervals between bins used to group data.

Table 4 Summary of daily average values for all three datasets

Weather Variable	Data Sets		
	2015++	2013-2016	2013-2014
Temperature ($\pm 1.0^{\circ}\text{C}$)	17–26	10–13, 23+	N/A
Relative Humidity ($\pm 5\%$)	70–90	>70	N/A
Wind ($\pm 2.0 \text{ km}\cdot\text{h}^{-1}$)	N/A	N/A	<10
Max Wind Gust ($\pm 2.0 \text{ km}\cdot\text{h}^{-1}$)	N/A	N/A	<35
Solar Radiation ($\pm 25 \text{ W}\cdot\text{m}^{-2}$)	200+	150+	N/A
Precipitation ($\pm 5 \text{ mm}$)	5–25	<25	N/A

The values for 2015++ were used as input for the Honey Optimal Flight Indicator (HOFI) set up as in **TABLE 5**. The 2013-2016 dataset was omitted due to having an irregular gap in the optimal daily temperature value that was not found in the literature.

Table 5 HOFI results using historical daily averages from January 1, 1981 to December 31, 2010 based on the reference data used in KNMI climate scenarios.

Temperature ($^{\circ}\text{C}$)	Relative Humidity (%)	Wind ($\text{km}\cdot\text{h}^{-1}$)	Max Wind Gust ($\text{km}\cdot\text{h}^{-1}$)	Solar ($\text{W}\cdot\text{m}^{-2}$)	Precipitation (mm)	Total Day Count
17–26	70–90	10	35	200	25	452

Note that in **TABLE 5** the values are not the total amount of productive honey bee days, but the amount of optimal productive days. The HOFI calculated 452 days out of 10,957 days to be optimal for honey bee flight. This is 4.1% of the time period. Based on these results, the estimated current amount of optimal productive honey bee days in the Netherlands is 15 days a year. The results of the sensitivity analysis are displayed in **TABLE 6** and shows that optimal honey bee flight appears to be predominantly limited by temperature (137% increase) followed by solar radiation (102%) and humidity (84%).

Table 6 Summary table showing the change in optimal honey bee flight days when one environmental criteria is removed, compared to the total using all criteria.

Amount of Days						
All	Without					
	Temp.	Humidity	Wind	Max Gust	Solar	Precip.
452	1071	833	519	452	915	456
Days per Year						
15	36	28	17	15	31	15
Change per Year from All (day)						
x	21	13	2	0	15	0
Without % Change from All						
x	137%	84%	19%	0%	102%	1%

Table 7 Simplified HOFI results using historical daily averages from January 1, 1981 to December 31, 2010 based on the reference data used in KNMI climate scenarios.

Temperature (°C)	Solar (W·m ⁻²)	Precipitation (mm)	Total Day Count
17–26	200	25	969

Table 8 Results of a sensitivity analysis for the simplified HOFI showing the change in optimal honey bee flight days when one environmental criteria is removed, compared to the total using all criteria.

Amount of Days			
All	Without		
	Temp	Solar	Precip.
969	2101	1589	975
Days per Year			
32	70	53	33
Change per Year from All (day)			
x	38	21	1
Without % Change from All			
x	117%	64%	1%

3.5 Future number of optimal flight days

TABLE 9 shows the differences in average optimal days per year for 2050 and 2085 for all scenarios. The greatest increase is seen in the WH (43%, 53%) scenario for both years (2050, 2085, respectively). Between years, the greatest average increase is seen in 2085 (38%) compared to 2050 (31%). Sensitivity analysis shows that this pattern persists when the temperature, solar, or precipitation criterion is excluded from the HOFI. For both 2050 and 2085, in all four scenarios the amount of optimal honey bee flight days increase compared to the reference period (**FIGURE 4**).

Table 9 Summary of HOFI sensitivity results using the transformed KNMI climate scenarios for 2050 and 2085 in the Netherlands.

Data set		Days Per Year				Day Change per Year from Reference				% Change Day per Year from Reference			
		All	Without			All	Without			All	Without		
			Temp	Solar	Precip		Temp	Solar	Precip		Temp	Solar	Precip
Reference		32	70	53	33	x	x	x	x	x	x	x	x
2050	GL	39	71	71	39	7	1	18	7	21	2	34	21
	GW	42	74	75	42	9	4	22	9	29	6	41	29
	WL	42	70	86	42	10	0	33	10	31	0	63	31
	WH	46	74	91	47	14	4	38	14	43	6	72	43
2085	GL	39	70	76	39	7	0	23	7	20	0	43	21
	GW	43	73	80	43	11	3	27	11	34	5	52	34
	WL	47	71	110	47	15	1	57	15	46	1	108	46
	WH	50	75	112	50	17	5	59	17	53	7	112	53

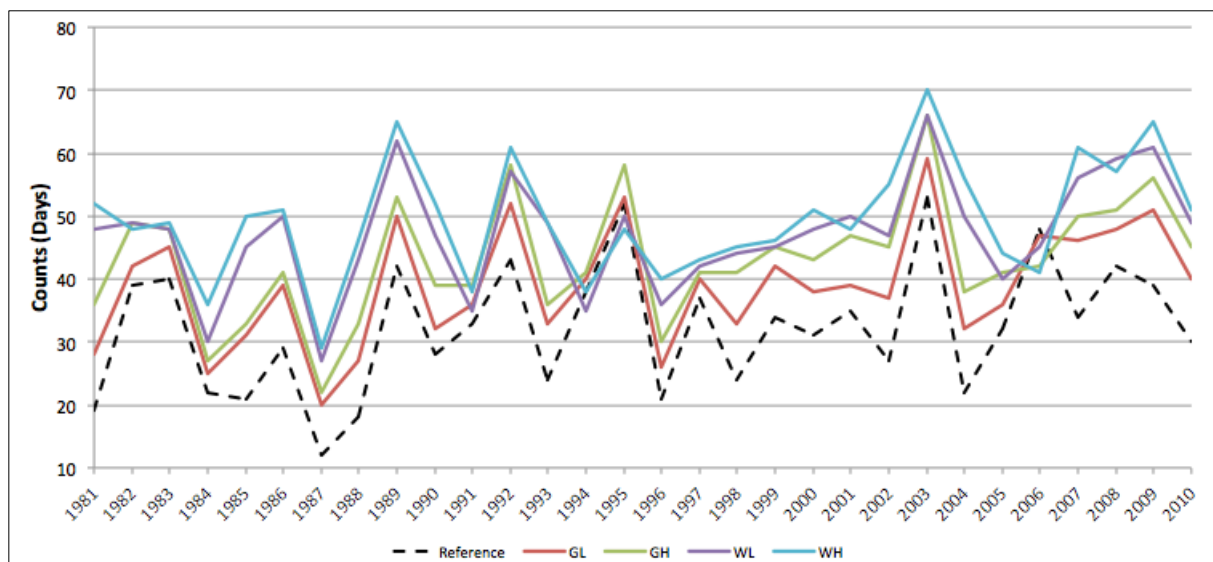


Figure 4 The simplified HOFI results for four scenarios in 2085 and the reference period showing predominantly an increase in optimal days for all scenarios. The graphs of 2050 and 2085 are visually similar so only 2085 is shown.

In determining empirically whether the future number of optimal flight days is the same as the current amount, an F-test was done to determine which t-test to conduct. The F-test revealed that we couldn't reject the notion that the variances are equal ($F \text{ value} < F \text{ critical}$) for all scenarios, resulting in the use of a two-sample t-test assuming equal variances. This test was used to reject the H_0 that the average number of optimal flight days (mean) from the reference data is the same as in each scenario with or without an excluded criterion (precipitation or solar radiation) ($|t \text{ stat}| > t \text{ Critical two-tail}$) with 95% confidence. I rejected the H_0 that the average number of optimal flight days (mean) from the reference data is the same as in 2085 WH when the temperature criterion is excluded ($|t \text{ stat}| > t \text{ Critical two-tail}$).

with 90% confidence. However, the H_0 that the average number of optimal flight days from the reference data is the same for both 2050 (GL, GH, WL, WH) and 2085 (GL, GH, WL) when the temperature is excluded could not be rejected ($|t_{stat}| < t_{Critical two-tail}$) with 90% confidence. In layman's terms, this means that the future number of optimal flight days is not different than the reference amount when temperature is not included in the HOFI for 2050 GL, GH, WL, WH and 2085 GL, GH, WL. The future number of optimal flight days IS different than the reference amount for periods and scenarios for all remaining criteria combinations. This means that the HOFI is sensitive to temperature.

3.6 The Dutch apiculture sector

3.6.1 Pollination service value

The Netherlands is a net importer of honey (Deloitte, 2013; Chauzat et al., 2013; Blacqui re et al., 2009) and the number of beehives is closely related to the amount of honey produced.

The basic summary of the literature is that the value of honey and honey products is low, but the value of the pollination service honey bees provide is high and European beekeepers are not given the importance they deserve in the agricultural sector (Blacqui re et al., 2009; Hein, 2009; Deloitte, 2013; Chauzat et al., 2013; Breeze et al., 2014). Of the 264 crops produced commercially in the European Union, 80% are dependent directly on insect pollinators (Chauzat et al., 2013). Hein (2009) found that at the national level, between 1%–16% of the agricultural value of a crop may be attributed to pollination services from insects. The Netherlands is not listed specifically, but the EU-15 and the United Kingdom both have 2% while France has 1% attributed value to insect pollination. The Netherlands could perhaps be in a similar range, though these values are based on studies from the 1980s and 1990s and so could very well be outdated by now. Unfortunately, this does not differentiate between wild and managed insect pollinators. Kleijn et al. (2015) found the approximately contributed value per hectare of grown crop by managed bees to be € 3000 from managed honey bees. In 2009 the value of these services in the Netherlands was approximated at €1 billion from honey bees and €187 million for other pollinators and the value of honey sales was about €3.8 million (Blacqui re et al., 2009).

The market for pollination services in Europe is not as developed as in the United States of America (USA), where beekeepers rent individual hives to farmers (Rucker et al., 2012). The market price for renting a hive fluctuates depending on the crop and on hive availability; the rental price of a hive for almond pollination rose from \$35 to \$150 from the 1990's to 2007 due to the decrease in colonies from CCD (Deloitte, 2013). The spread of a pollination market in the USA may be due to a difference in pollinating services versus collecting nectar to produce honey, so when American beekeepers move their hives to almond orchards, they

must be compensated as little nectar is collected from almond trees (Ibid.). Blacqui re et al. (2009) propose a similar approach of separating pollination services and honey production to increase and improve the Dutch pollination market. In Germany, the market price for renting colonies works out to €20 per colony for rape crops and €50 per colony in orchards (Deloitte, 2013). In the Netherlands, hives are rented at €40–€50 per colony for fruit pollination, with 5000 colonies being used (Blacqui re et al., 2009). The market value of pollination (fees) in the Netherlands for honey bees was estimated at €10 million in 2009, but the actual value to the agricultural sector was €1.1 billion, not including pollination of non-agricultural plants, such as public green spaces (Ibid.). Therefore, this number should be taken as a minimum estimate for the Netherlands.

Given that the estimated value of pollination services by honey bees in the Netherlands is at least €1.1 billion, that the pollination market is worth €10 million, and that honey sales are €3.8 million, the approximate total economic impact of honey bees is, therefore, €1.114 billion (€1 113 800 000).

3.6.2 Trends

The Dutch apiculture sector is in poor shape compared to other European countries. In a report studying the demographics of the European apiculture industry, the Netherlands was found to produce 5kg of honey per hive compared to the average of 16kg of honey per hive, making its hives the least productive out of all EU-27 (+ Norway and Kosovo) members (Chauzat et al., 2013). It also had a lower yield per 100km² with 1 tonne of honey, compared to an average of 4.8 tonnes (Ibid.). There are a few reasons for this. Dutch beekeepers are predominantly non-professional (99%), and of these 5% are part-time with the remaining 94% being hobby beekeepers. This leaves 1% as professional beekeepers, which is defined as one whose main income is from beekeeping (Ibid.). There are approximately 80, 000 hives in the Netherlands and vast majority (95%) of Dutch beekeepers have less than 50 colonies (Ibid.). This makes the density of hives per insect pollinated crop hectare to be 2.1, but studies show that 3 colonies per hectare are better for pollination and yields (Breeze et al., 2014).

Another difficulty is that the number of Dutch hives and beekeepers are decreasing (Blacqui re et al., 2009). More than 50% of European beekeepers are over 55 years, and though no data is available for Dutch beekeepers (Deloitte, 2013), it is probable that this is true for the Netherlands as well. Blacqui re et al. (2009) state that since Dutch beekeepers are aging and the sector is predominantly considered a hobby, beekeepers are not being replaced. There is also the issue that in the Netherlands beekeeping is no longer profitable (Blacqui re et al., 2009), but whether this is because most are hobbyists and do not have the economies of scale is unknown. There is difficulty in addressing the threat of Varroa mites

without compromising the quality of honey due to miticides (chemicals that kill mites) (Blacqui re et al., 2009). The cost of treating beehives against diseases can now lead to a net loss for beekeepers and with difficulty putting products on the market and having to compete with cheaper imported honey, there is a decline in beekeepers who no longer find it profitable (Deloitte, 2013). Continuous and varied supply of pollen is needed for optimal bee health – this is easier to achieve in cities due to the large variety of plant species found within urban areas, compared to the monocultures in rural areas (Blacqui re et al., 2009). However, this is becoming a liability issue for beekeepers, for if someone is stung the beekeeper is likely to be held responsible if hives are kept near people (Ibid.).

More development of pollination markets in the Netherlands is unlikely until the agriculture sector starts to understand the true value of the pollination service that honey bees provide (Blacqui re et al., 2009). Blacqui re et al. (2009) propose that this is a result of a general mind-set that pollination has always happened so why to start paying for it now and that beekeepers sell the honey their bees gather, so they should not be paid to collect that honey. This mind-set may change in the future with the decline of wild pollinators, as Jaff  et al. (2010) suggest that managed honey bees are currently not replacing the pollination services lost from the disappearance of wild pollinators, thus leading to an increased demand for honey bee pollination services.

3.7 Future economic value of honey bee pollination services

The economic impact of honey bees in the Netherlands is estimated to be €1.114 billion. The current number of optimal honey bee flight days in the Netherlands is 32, and this is expected to vary between 39–46 by 2050 and 39–50 by 2085. The economic value of honey bees in the Netherlands is expected to increase given that honey bee flight days are predicted to increase, based on the KNMI scenarios. **TABLE 10** shows how the economic value of honey bees will increase for both time periods and all scenarios. The greatest increase is seen in the WH scenario (191% by 2050, 946% by 2085) and the lowest is in the GL scenario (21% by 2050, 250% by 2085).

Table 10 The potential change in the economic impact of honey bees per year in the Netherlands due to climate change. Values for scenarios were calculated based on the cross-ratio of current optimal days, the estimated economic value of honey bees in the Netherlands in 2009, and the estimated optimal days for each scenario.

Data set		Economic Value of Honeybees per Year (€ billion)	Change per Year from Reference (€ billion)	% Change Economic Value per Year from Reference
Reference		1.11	x	x
2050	GL	1.34	0.23	21
	GW	1.73	0.62	55
	WL	2.26	1.15	103
	WH	3.24	2.13	191
2085	GL	3.90	2.79	250
	GW	5.21	4.10	368
	WL	7.60	6.49	582
	WH	11.65	10.53	946

The Netherlands is a large global player in agriculture export, with 80% going to EU members, and its agricultural complex²¹ contributed almost 10% to the total GDP in 2011 (OECD, 2015). Forty-three percent of the Netherlands is used for agriculture, lower than the EU15 average of sixty percent, but the Netherlands has very high agricultural yields per hectare in comparison to other countries. Productivity has increase by 2.6% on average per year since 1961 (Ibid.). However, the Netherlands has had difficulty in reducing the environmental impact of its agriculture sector while maintaining or increasing productivity (Ibid.). The Dutch agricultural sector also faces risks due to price volatility, water shortages, and possible flooding due to climate change as well as increased competition for land use (Ibid.). More than half of the land used to generate two-thirds of the Netherlands' Gross Domestic Product (GDP) is located in flood prone areas (Slomp, 2012) so flooding in this region will have serious economic repercussions on the Dutch economy. Crop yield losses are expected to occur due to droughts and infrequent precipitation; shipping via waterways will become costlier and more difficult due to lower river levels (Ligtvoet et al., 2015). Food prices are expected to rise due to consecutive periods of drought (Ibid.). Mitigation costs due to climate change may be high, using funds that may have gone towards improving the production scale or farming practices (OECD, 2015). Periods of extreme heat or drought also impact beekeeping activities (Epstein et al., 2013). Honey bees will cease foraging and will search for water sources to cool themselves and the hive to prevent heat exhaustion and death (Crane, 1990). Beekeepers are recommended to supply their hives with sources of

²¹ Defined as "primary production, processing, input manufacturing and distribution" (OECD, 2015, pg. 36)

water as well as supplementary food as flower blossoms may be dried out making collecting nectar and pollen impossible for bees (Epstein et al., 2013).

4 Discussion

4.1 Research Question 1

The choice to conduct a literature review proved fruitful thanks to the large amount of published studies and allowed for a thorough investigation into how weather factors influence honey bee flight. The results have shown that the known environmental conditions conducive for honey bee flight for pollination purposes are temperature, relative humidity, pressure, solar radiation, light intensity, precipitation, and wind. Ranges for most of these weather conditions were identified but as Hepburn and Radloff (2011) eloquently put it, “foraging activity in bees may be a consequence of several interacting factors in which the value of one factor with high values may compensate for lower values of the other factors” (pg. 271). This means that it is possible for honey bees to forage under certain sub-optimal conditions if other conditions allow and the cost vs. benefit results for nectar are positive. An example of this is honey bee basking when it rests in sunlight to warm up to appropriate flight temperature; without solar radiation, the honey bee is dependent on higher ambient temperatures for flight (Willmer & Stone, 2004). Another example is of honey bees using the force of the wind to use less energy in flight either coming from or to the hive (depending on wind direction) (Crane, 1990). There are however limits at which compensation cannot occur, thus becoming limiting factors. To illustrate, in winter the limiting factor for honey bee flight is temperature, while in summer it is predominantly light intensity and solar radiation (Hepburn & Radloff, 2011).

Despite coming across numerous references that honey bees do not fly in the rain, I did not find any scientific studies to quantify this. Therefore a big gap in the literature exists for this weather condition. For future research, I would recommend to thoroughly investigate at what precipitation amount honey bee foraging starts to be impaired. Perhaps this is a simple case of physics where the force of falling rain drops increases flight energy requirements, or maybe the honey bee risks losing too much heat from being wet, becoming stranded outside the hive until it dries off and is able to warm up again for flight. Both could be reasons why flying in rain could be energetically unprofitable for honey bees. In a rainy country like the Netherlands, this information could be useful to identify sub-par conditions for pollination and empower beekeepers and farmers to make better pollination decisions such as increasing hive density or growing different crops.

4.2 Research Question 1a

The purpose of this question was to determine how well weather and hive weight or hive weight change can be used as an indicator for colony productivity. The extent of the known weather conditions conducive for honey bee flight for pollination purposes correlated on average $\tau = 0.13$ to hive weight and $\tau = 0.04$ to change in hive weight. This is unexpectedly low

compared to Marceau et al.'s (1990) value of $r^2 = 0.79$ and Szabo's (1980) value of $r^2 = 0.77-0.88$ between honey bee flight activity and hive weight (honey production), though their studies were conducted for different purposes and with different methodologies compared to this one. Both Marceau et al. and Szabo had different sampling times (daily over the period of a summer, one-day sampling during beginning, peak, and end of nectar flow for three consecutive years, respectively) whereas this study looked at the whole possible flight season for bees. The whole flight season was used in this study to determine the optimal weather conditions for foraging, something which neither Marceau et al. (1990) nor Szabo (1980) attempted to do. Szabo did find a correlation between weight gain with flight activity, temperature, relative humidity, wind speed, and light intensity ($r^2 = 0.490-0.837$), but did not list the direct correlation between hive weight and the weather factors, so it is difficult for outright comparison. There is also difficulty in comparing parametric (r^2) with non-parametric (τ) values. A future analysis could be done using only data from the period of the nectar flow, or during the summer months to better compare with Marceau et al.'s (1990) and Szabo's (1980) studies.

4.3 Research Question 1b

The optimal weather conditions conducive for honey bee flight for pollination purposes based on field data were identified in **SECTION 3.3**. Comparing literature findings (**TABLE 1, pg. 23**) with the observed results is unfortunately difficult, as the results show weather conditions under which a colony is seen to be thriving, but not at what weather conditions foraging commences, peaks, or ends. However, we may gather when peak foraging conditions for the (>46kg) group are, based on when the fraction of (>46kg) occurrences are the greatest (i.e. when the (46kg) line is higher than both (<44kg) and ($\geq 44\text{kg}, \leq 46\text{kg}$)). For temperature, the datasets 2015++ and 2013-2016 match Rohnstock's (2011) value of 12°C. Paired 2013-2016 falls into the range of Vicens & Bosch (2000) and Kevan & Baker's spring value (1983) and matches the value of Abrol (2015). Paired 2013-2016's end value of 27°C corresponds to the peak foraging value for Puškadija et al. (2007). Paired 2015++ falls into the May range of Kevan & Baker (1983). The humidity starting values for all datasets fall short of Puškadija et al.'s (2007) initial value of 40%, and include a much wider range (30–100% vs. 40–50 %, 65–75% (Puškadija et al., 2007)) though with the margin of error, Paired 2015++ could overlap to Puškadija et al.'s (2007). No literature values for pressure were found, but all four data sets had starting values of 100.6kPa or 100.7kPa. The paired datasets had the same ending value of 101.0kPa while the unpaired datasets varied by 0.3kPa. A low pressure usually indicates cloudy or stormy weather, while high pressure tends to indicate clear, sunny

skies.²² Solar radiation values are all higher than the given literature values (**TABLE 1**), though the Paired 2013-2016 start value of 325 comes close to the 300 of Vicens & Bosch (2000). Again, these optimal values are not based on when foraging commences but when the frequency of (>46kg) displays a sustained increase. All datasets did not have an endpoint, which counters literature findings, which state there is a negative quadratic relation between solar radiation and flight activity (Burrill & Dietz, 1981; Meikle & Holst, 2015). Wind values varied between 2013-2014 and Paired 2013-2014 by 2km and straddled the 11 km·h⁻¹ value of Kevan & Baker (1983). The wind gust values, although not explicitly searched for in the literature, do fall below Kevan & Baker's (1983) upper foraging limit threshold of 24–34 km·h⁻¹. What is odd is that the Paired 2013-2014 dataset shows a minimum wind gust value. Nowhere in the literature was a minimum wind/gust speed stated, and I had assumed it to be 0 km·h⁻¹, but perhaps a mild wind is preferred for bee foraging.

Delta weight is likely to have been influenced by humidity, wind, and precipitation, and while these factors also influenced hive weight, they possibly have had a less pronounced impact, as the range of hive weight values is larger. Delta weight has a range of -1kg to +1kg, whereas hive weight can vary from 23kg to 163kg. This results in weather variables having a lesser chance of creating a compounding effect and thus leads to a stronger signal.

The accuracy of the optimal values may be called into question as the correlation between hive weight and weather factors is only 0.433 (Multiple r) (2015++ dataset) indicating that another factor or other factors have a greater influence upon hive weight than weather conditions. This is understandable since the method assumes nectar sources are always present in the same concentrations, and that honey bees are only being prevented from foraging by weather conditions. However, this is not the case. Bees have evolved to forage when flowers are present if it results in a net energy benefit and as such, no phenological mismatch has been found between flowering times and bee pollination (of all bee species) (Forest, 2014). Flowers have also co-evolved to bloom at temperatures when bee species are present for foraging (Ibid.). As for the assumption that nectar sources always contain the same concentrations, it is irrelevant to my model as once the >46kg threshold is reached, it does not matter by how much it increases or decreases so long as the hive weight stays within the >46kg weight class.

The ad hoc rule to exclude bins that contained less than one percent of the total number of counts, as well as the actual bins themselves may have skewed the results, especially for pressure. **TABLE 11** shows that almost half of all pressure bins (41–44%) were removed due to

²² <http://www.metoffice.gov.uk/learning/learn-about-the-weather/how-weather-works/highs-and-lows/pressure>

the 1% ad hoc rule. It also shows that almost half or more than half of wind or wind gust bins (42–60%) were removed due to the same rule. The high number of discarded bins may appear to be problematic. However, **TABLE 12** shows that the removal of the bins for wind and wind gust only discarded 1–3% of data points, whereas with pressure this amount is much larger falling between 5–11%. First, this means that the number of bins removed are not necessarily be problematic. Second, this does indicate, however, that the bin categories for pressure (increasing by 0.1kPa per bin) was inappropriate and should have been increased by larger intervals (perhaps 0.2kPa) to reduce the amount of data points that were discarded. The removal of so many data points from pressure likely led to the difficulty in identifying a clear signal when analysing the data for starting points for optimal flight conditions.

Table 11 Summary of total and removed bins per weather condition in determining optimal flight conditions due to the ad hoc 1% rule

Dataset	Bins						
	All	Removed					
		2015++	Paired 2015++	2013-2016	Paired 2013-2016	2013-2014	Paired 2013-2014
Temperature	35	4	3	5	4	x	x
Relative humidity	21	0	0	5	5	x	x
Wind	20	x	x	x	x	12	8
Wind gust	26	x	x	x	x	12	11
Pressure	39	16	16	17	17	x	x
Solar radiation	37	1	3	1	3	x	x
Dataset		% Bins removed					
Temperature		11%	9%	14%	11%	x	x
Relative humidity		0%	0%	24%	24%	x	x
Wind		x	x	x	x	60%	40%
Wind gust		x	x	x	x	46%	42%
Pressure		41%	41%	44%	44%	x	x
Solar radiation		3%	8%	3%	8%	x	x

Table 12 Summary of total and removed data points per weather condition in determining optimal flight conditions due to the ad hoc 1% rule

Dataset	Data points						
	All	removed					
		Temperature	Relative humidity	Wind	Wind gust	Pressure	Solar radiation
2015++	32305	407	0	x	x	1762	179
Paired 2015++	31352	387	0	x	x	1947	540
2013-2016	68981	1016	1251	x	x	3448	308
Paired 2013-2016	67385	959	1172	x	x	3258	926
2013-2014	37876	x	x	854	768	x	x
Paired 2013-2014	37226	x	x	448	925	x	x
Dataset		% removed					
2015++		1%	0%	x	x	5%	1%
Paired 2015++		1%	0%	x	x	6%	2%
2013-2016		3%	4%	x	x	11%	1%
Paired 2013-2016		3%	4%	x	x	10%	3%
2013-2014		x	x	3%	2%	x	x
Paired 2013-2014		x	x	1%	3%	x	x

4.4 Research Question 2

The current number of optimal honey bee flight days in the Netherlands based on daily temperature, relative humidity, solar radiation, precipitation, wind, and maximum wind gust is 15 days a year. Using only daily temperature, solar radiation, and precipitation as criteria this number increases to 32 days a year. This is likely the result of omitting predominantly relative humidity and to a lesser extent wind, as shown by the sensitivity analysis in **TABLE 6 (PG. 31)** with an increase of 84% in optimal flight days when the humidity criterion is removed and a 19% increase when the wind criterion is removed.

Unfortunately, no literature values for optimal honey bee flight daily averages could be found, as weather values were recorded only at the time of sampling; therefore, no direct comparison can be done with the experimental values. Taking the 2015++ and daily 2015++ optimal points, the temperature and relative humidity values are much higher in daily 2015++ (17–26°C vs. 12+°C, 70–90% vs. 30+%) whereas the solar radiation value is higher in 2015+ (525+ W·m² vs. 200+ W·m²).

In comparing the 2015++ and 2013-2016 datasets, the temperature had different starting points, with 2013-2016 having a lower start value accompanied by a gap not seen in 2015++. This gap is a result of the used definition of a clear and sustained positive or negative increase. For relative humidity, both data sets closely overlap, but an upper limit was identified in 2015++. Solar radiation values differ, which may be accounted for by 2015

having a lower yearly average value of 148.4 W·m⁻² compared to 191.25 W·m⁻² for 2014²³; this lower yearly average has likely pushed the optimal threshold higher if there were less sunny days compared to 2014. Values for both sets overlap if we consider the margin of error.

Precipitation values differ, which may be accounted for by 2015 having a higher yearly day average value of 1.29 mm compared to 1.05 mm for 2014²⁴. This higher daily probably pushed the optimal threshold lower if there were rainier days compared to 2014. Both daily precipitation values are higher than Rohnstock's (2011) daily value of 1 mm threshold, though Rohnstock's value appears to be based on an ad hoc rule rather than data analysis.

The chosen bins and ad hoc rule of discarding bins that contained less than 1% may have skewed the results as discussed in **SECTION 4.3** but while **TABLE 13** shows bin removals of 38–54% for precipitation, this translates to 2–5% of discarded data points (**TABLE 14**). This indicates that the bin groupings for the different weather conditions were appropriate.

Table 13 Summary of total and removed bins due to ad hoc 1% rule in determining daily optimal flight conditions

Dataset	Bins						
	All	Removed			% Bins Removed		
		2015++	2013-2016	2013-2014	2015++	2013-2016	2013-2014
Temperature	35	4	5	x	11%	14%	x
Relative humidity	21	5	5	x	24%	24%	x
Wind	6	x	x	1	x	x	17%
Max wind gust	12	x	x	2	x	x	17%
Solar radiation	21	5	7	x	24%	33%	x
Precipitation	13	7	5	x	54%	38%	x

Table 14 Summary of total and discarded data points due to the ad hoc 1% rule when determining daily optimal flight conditions

Dataset	Data points						
	All	Removed					
		Temperature	Relative humidity	Wind	Max wind gust	Solar radiation	Precipitation
2015++	434	9	9	x	x	4	20
2013-2016	836	30	9	x	x	11	14
2013-2014	403	x	x	3	2	x	x
Dataset		% Removed					
2015++		2%	2%	x	x	1%	5%
2013-2016		4%	1%	x	x	1%	2%
2013-2014		x	x	1%	0%	x	x

A criticism of the HOFI may be that equal weight is given to all weather factors although temperature has historically been assumed to be the most dominant factor (**SECTION 3.1.4.1**) and was identified in **TABLE 6 (PG.31)** as the greatest limiting factor in the HOFI. However, plotting the count of optimal flight days per year shows an unusual pattern

²³ Yearly solar radiation values unavailable at wunderground.com; pivot table values used.

²⁴ Yearly daily precipitation values unavailable at wunderground.com; pivot table values used.

(**FIGURE 5**). The pattern is unusual due to a sharp decrease in optimal day counts from 2002 to 2006 that is not accompanied by a sharp decrease in yearly average temperature. One would expect optimal flight days to be steadily increasing from 2004 to 2006 as the yearly average temperature increases, and decrease when temperature decreased between 2007–2009, but this did not happen. **FIGURE 5** is showing a different story than what the literature and sensitivity analysis suggests. Other weather factors may be having a greater influence – This is discussed in **SECTION 7.1**. As an interesting side note, the decline in optimal flight days almost seems like a precursor to when the first cases of Colony Collapse Disorder started becoming prevalent in 2005–2006. Future studies could be done to see if optimal flight days per year correspond to historical colony amounts.

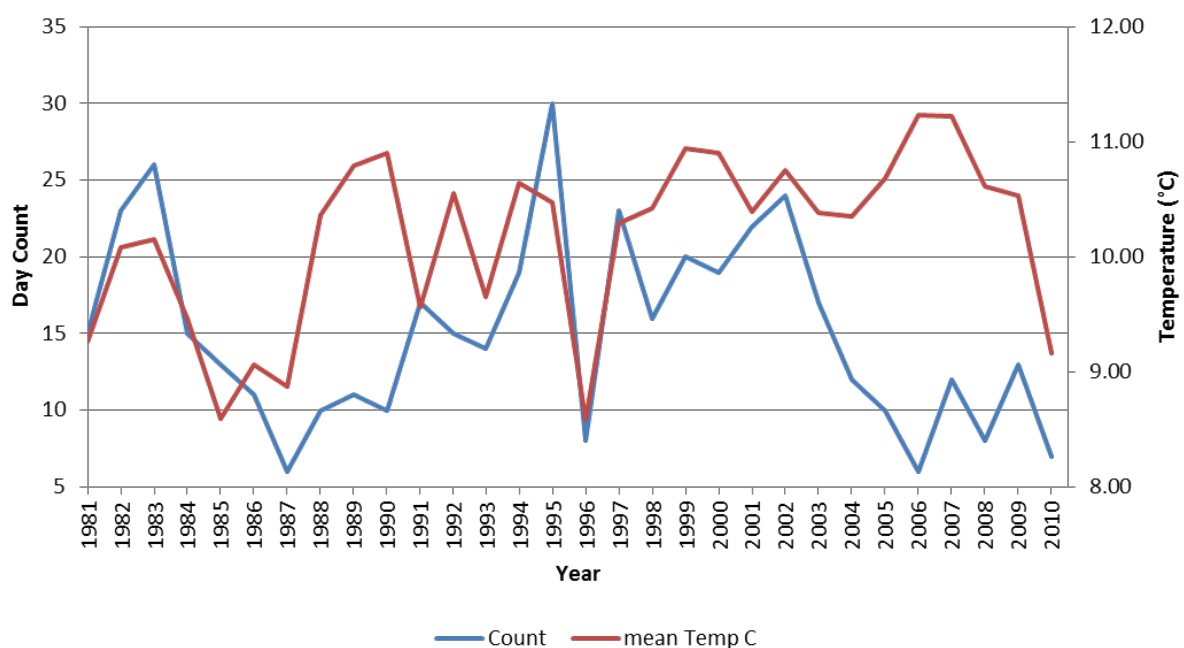


Figure 5 The amount of optimal honey bee flight days per year from 1981 - 2010 using temperature (°C), solar radiation, wind, maximum wind gust, precipitation, and relative humidity. The average yearly temperature is also shown.

4.4.1 Model Validation

The HOFI model should be validated to show that it is acceptable for predicting the amount of honey bee optimal flight days in a year (Rykiel, 1996). To be considered acceptable, I would like it to have an accuracy score of 90% in predicting the amount of honey bee optimal flight days in a year. This may be done by (ideally) taking the daily averages of the temperature (°C), relative humidity (%), wind ($\text{km}\cdot\text{hr}^{-1}$), wind gust ($\text{km}\cdot\text{hr}^{-1}$), solar radiation ($\text{W}\cdot\text{m}^{-2}$), and precipitation (mm) for a different hive, and follow the relevant steps in **SECTION 2.3**. The count predicted by HOFI should then be compared to the count of days for when the different hive had a weight of 46kg or more. Another way to validate it is using data from the same hive (Athens, Georgia, USA) using the same procedure. A different hive is

preferred since the HOFI is based on the Athens hive and so may display an accuracy bias towards it.

4.5 Research Question 3

The number of days with favourable honey bee flight conditions for pollination in the Netherlands under the different future climate change scenarios as used by KNMI varies between 39–46 around the year 2050 and 39–50 around the year 2085.

The column where the solar criterion is excluded shows the greatest increase (34–112%) in the optimal days per year compared to the reference period. This would suggest that solar radiation is currently a limiting factor in the Netherlands. Solar radiation is expected to rise according to the KNMI scenarios, which is likely driving the increase observed. Perhaps in the future, an upper threshold limit for solar radiation will be determined, as the literature describes the existence of one (**SECTION 3.1.4.4**).

The methodology for establishing optimal honey bee flight conditions and using these conditions as criteria to determine if optimal flight conditions increase or decrease in the future appears rather straight forward but no studies with a similar set up have been found. As mentioned in the introduction, I came across two studies that investigated the potential impact of climate change on honey bees. Rader et al. (2013) used two different scenarios from the 2007 IPCC report, but only focused on temperature changes. They found that under the most extreme IPCC scenario, pollination services by honey bees are expected to decline by 14.5% (Rader et al., 2013). Their study design was based on the number of honey bees found in flowering watermelon fields correlated with temperature, with measurements taken when watermelon flowers were open; they did not indicate the density of hives in the fields (Ibid.). Delgado et al. (2012) also used two scenarios from the 2000 IPCC report and found that honey yields are likely to be reduced due to temperature and precipitation changes (Delgado et al., 2012). They did note that their models were only able to explain 53% of the variability in honey yields (Ibid.). Both these studies have opposite results from my findings, which may be due to differences in methodology. Rader et al. (2013) used hourly temperatures paired with visual inspection of transects to determine bee visits per flower followed by catching and identifying bees. Field visits did not occur under rainy conditions and the vast majority (90%) of data collection took place when winds were less than 2.4 m s^{-1} . Delgado et al. (2012) used various models based on yearly, monthly, or quarterly (three months) variables of mean, minimum, and maximum temperatures, and the annual, wettest, or driest, coldest or warmest quarter for precipitation. Different time scales make it difficult to compare my results with these studies.

4.6 Research Question 4

The current economic importance of the Dutch apiculture industry according to Blacqui re et al. (2009) is estimated to be  1.114 billion, and the current trends in this industry are a decline of beekeepers, a poor pollination market, and sub-par honey yields compared to other EU states.

The results of the Dutch literature review are weak due to little available data. Results for the economic impact of honey bees in the Netherlands are difficult to obtain due to poor statistical records. As a result, I widened my search to neighbouring European countries such as Germany. Although there was little Dutch data, the data found did correlate with the more robust observed trends in other European countries, indicating a clear trend. I encountered several issues while trying to collect Dutch statistical data. Statistics Netherlands (CBS) does not collect separate information on the consumer price of honey in the Netherlands. It is grouped together with jams and marmalade²⁵; yearly Netherlands imports/exports are grouped with eggs and dairy²⁶; and international import/exports are grouped with sugar, molasses, or powdered sugar.²⁷ FAOStat findings have different time scales, ending at 1987 or 2013, and data is missing when compared to other European countries, such as the export or import of beehives. Statistical data from EuroStat for the apiculture sector for Netherlands is even scarcer. No information could be found when searching honey or beehive or beekeeper for the Netherlands. As a result of these issues, as previously mentioned, I was forced to expand my search to neighbouring countries as well as determine general European trends.

If the Dutch government would like to develop a beekeeping developmental program, a better assessment of beekeeping trends in the Netherlands is essential to determine which issues to focus on. This can be done by gathering yearly statistics regarding the numbers of beekeepers and hives, the expenditure and income of professional and hobby beekeepers, the average price of the pollination market, and the area or economic value of crops pollinated by honey bees. This could be done either through a census or through the different beekeeping associations in the Netherlands. The income of Dutch beekeepers could be improved by either increasing the amount of hives owned or as Blacqui re et al. (2009) suggests, separating honey production from pollination services. That is, either the focus should be on producing honey or providing pollination services.

²⁵ <http://statline.cbs.nl/Statweb/publication/?DM=SLNL&PA=83131ned&D1=0-1,4-5&D2=51>

²⁶ <http://statline.cbs.nl/Statweb/publication/?DM=SLNL&PA=83180ned&D1=49,106,163,220>

²⁷ <http://statline.cbs.nl/Statweb/publication/?DM=SLNL&PA=7137shih&D1=0-2&D2=34-35&D3=0-2&D4>

4.7 Research Question 5

To determine the rough estimate optimal day value by dividing the total economic impact of honey bees in the Netherlands by the number of optimal flight days in a year is tempting, but this would be a misrepresentation of the estimated total economic impact value. This value was calculated only for one year (2009), whereas the results of the HOFI are the average over a 30-year time span (1981–2010). I could compare no prior values to determine if this value is increasing or decreasing. The used values must thus be considered a snapshot.

But whether the increase in optimal flight days will translate to an increase in pollination potential remains to be seen. The assumption of socio-economic factors remaining constant for the next 50–80 years based on the trends identified in **SECTION 3.6.2** is unlikely.

Knowing that the average number of optimal flight days in the Netherlands will increase in the future and that the Dutch agriculture sector will continue to grow, the pollination potential and the economic value of pollination service should increase in theory. But this may not be the main reason for the increase in economic value. If crop failure is expected to occur due to climate change (Ligtvoet et al., 2015) resulting in an increase in food prices, the economic importance of honey bees will increase as the economic value of honey bees is based on the value per hectare of grown crop by managed bees (as calculated by Kleijn et al. (2015)). Crop failure can increase demand for honey bees to ensure what crops remain are fully pollinated as farmers try to recoup their losses. As crop failures are predicted to be linked to periods of drought (Ligtvoet et al., 2015) this would also indicate that hives are in danger of overheating or starvation (Epstein et al., 2013) adding to the complexity and cost of pollination services. If there are less hives, then as the demand for hives increases and the supply of them decreases, the prices for hive rental will increase similar to in the USA when prices rose almost five-fold due to the decrease in colonies from CCD (Deloitte, 2013). Since there are very few Dutch commercial beekeepers and the amount of Dutch beekeepers is decreasing (Blacquière et al., 2009), the honey bee pollination service market may become oligopolistic (a small number of individuals/companies exert large impacts on a market).²⁸ Under an oligopolistic situation, the economic value of honey bee pollination services may not necessarily reflect the true cost of the market then. However, in the future it may become economically inviable to produce crops in the Netherlands resulting in the import of commercial crops. If this occurs, the demand for pollination services would decrease dramatically and the economic importance of honey bees would decline. This, however, would be an extreme adaptation measure and would likely not be supported by the government or populace.

²⁸ <http://www.merriam-webster.com/dictionary/oligopoly>

5 Concluding Remarks

The honey bee is a complex organism capable of adapting to changing weather conditions based on energy-efficiency. The seven weather factors identified in the literature seem to carry varying influences with temperature assumed to be of primary importance, though solar radiation has also shown to exert a large influence. The hive weight correlates more strongly with weather conditions compared to change in hive weight, but the percentage is low due to my data having a non-normal distribution. Nonetheless, optimal flight conditions could still be identified and these were generally corroborated with literature values. In obtaining the daily values, this study ventured into unknown territory as I could not find values to compare to, nor was I able to validate the newly constructed HOFI model. In determining the optimal flight days for the Netherlands to be 32 days a year, I was quite surprised and assumed it must have been due to the (usually) constantly changing Dutch weather. I was heartened to see an increase in the future may occur due to climate change, as the poor state of the Dutch apiculture industry suggests that it would benefit from climate change. Nonetheless, I have been able to answer this thesis' original question: in theory the number of optimal flight days is expected to increase due to climate change, but the predicted increase in the value of pollination services will more likely be a result of the open market and increased demand due to predicted crop failures.

The results of this thesis are useful for both Dutch beekeepers and the government. Although at first glance beekeepers and government have different interests (honey production vs. agricultural output) they are intertwined. As mentioned previously, agricultural output is dependent on or is improved by animal pollination, and so if the government's goal is to increase output it needs to ensure there is sufficient supply of pollination services in the future. It is therefore in the government's best interest to reverse the trend of declining beekeepers and colonies. Beekeepers in turn need to realize the vital importance of, and to modernize their trade. By increasing their own knowledge, beekeepers will be in a better position to negotiate pollination service fees, thus increasing their own income.

This thesis is interesting for a few reasons. I combined different types of data that previously never have been combined. Previous studies had not specifically tested the correlation between hive weight and weather conditions, usually using hive entrance activity and weather instead. I have not found studies that tried to determine optimal flight conditions using a vast amount of daily data over two or three years. Most were done using a day or two of observing the hive entrance and taking weather measurements. The advent of the electronic hive scale will likely usher in new, less labour-intensive and less costly studies, that perhaps will follow in a similar vein.

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Winning, invoer en uitvoer van materialen naar soort; nationale rekeningen.
<http://statline.cbs.nl/Statweb/publication/?DM=SLNL&PA=8318oned&D1=49,106,163,220>

7 ANNEX I

7.1 Further Analysis

A way to determine if different weights should be added to the HOFI or if temperature is indeed a limiting factor, a path analysis could be conducted. Abrol (2006) suggests using path coefficient analysis, as it shows the strength and significance of connections between variables (causes and effects). Path coefficient analysis is an extension of multiple regression, which breaks down the contribution of the r^2 value of each independent variable from a multiple regression into their direct and indirect influences on the dependent variable.²⁹ Another reason for choosing to use a path coefficient, as opposed to a path regression coefficient is that path coefficients are based on correlations and not regressions, which is more fitting for our data as the weather variables are known to not have linear relationships with honey bee flight (**SECTION 3.1.4, PG 24**) (Ibid.). The benefit of this analysis is that it may allow us to generalize the causes and effects between different independent variables as it shows causal relationships, however it does not prove them, as this needs to be tested experimentally (Ibid.).

To do a path coefficient analysis, the standardized beta coefficient of each independent variable to the dependent variable, and the correlation coefficients between independent variables is needed.

Standardized beta coefficients and correlation coefficients were taken from SPSS based on the data from 2013-2014 since they contained reliable wind data. The correlation coefficients were obtained using Kendall's Tau.

Steps for Path analysis

Get r^2 value for each independent variable and dependant variable to confirm linear correlation (needed for path coefficient analysis).

In SPSS:

Determine Standardised Coefficient

Analyse -> Regression -> Linear ->

Input hive weight (Y) as dependent, other variables (X) as independent

Record Standardized Coefficient for each X variable

Record r^2 value of all independent variables on a dependant variable

Determine Correlation between X variables

Analyse -> Correlate -> Bivariate -> Select Kendall's Tau

Record correlation between each independent variable (i.e. X1 & X2, X1 & X3 etc.)

In Excel:

²⁹ <http://faculty.cas.usf.edu/mbrannick/regression/Pathan.html>

Create formula:

$Y = (\text{standardized coeff } X_1) + \dots + \varepsilon$ where $\varepsilon = 1 - r^2$ (ε (epsilon) is the unaccounted influence on Y)

Determine Direct and indirect impacts of each independent variable

Direct impact

= Standardized coeff X_1 * Standardized coeff X_1

Indirect impact

= Standardized coeff X_1 * Standardized coeff X_2 * correlation between X_1 &

X_2

Total Indirect Impact of X_1 is summation of all X_1 Indirect Impact

Total Impact of X_1 is Direct impact plus Total Indirect Impact

Total Impact of all independent variables is the summation of Total Impact of all independent variables ($X_1 + \dots X_n$) and will equal the r^2 .

A path analysis diagram (**FIGURE 6**) was constructed from the Excel table, to better visualize the relationships between weather variables. The figure shows that temperature actually has a very minimal total impact (-0.01 or -1%) while solar radiation has the highest total impact (0.18 or 18%) on hive weight. This may be unusual but it is similar to what Abrol (2006) and Abrol & Kapil (1986) found. Based on this, we could propose that the criteria range for the HOFI variables of temperature, relative humidity, average wind speed and precipitation be widened while values for maximum wind gust and solar radiation should be narrowed in the future.

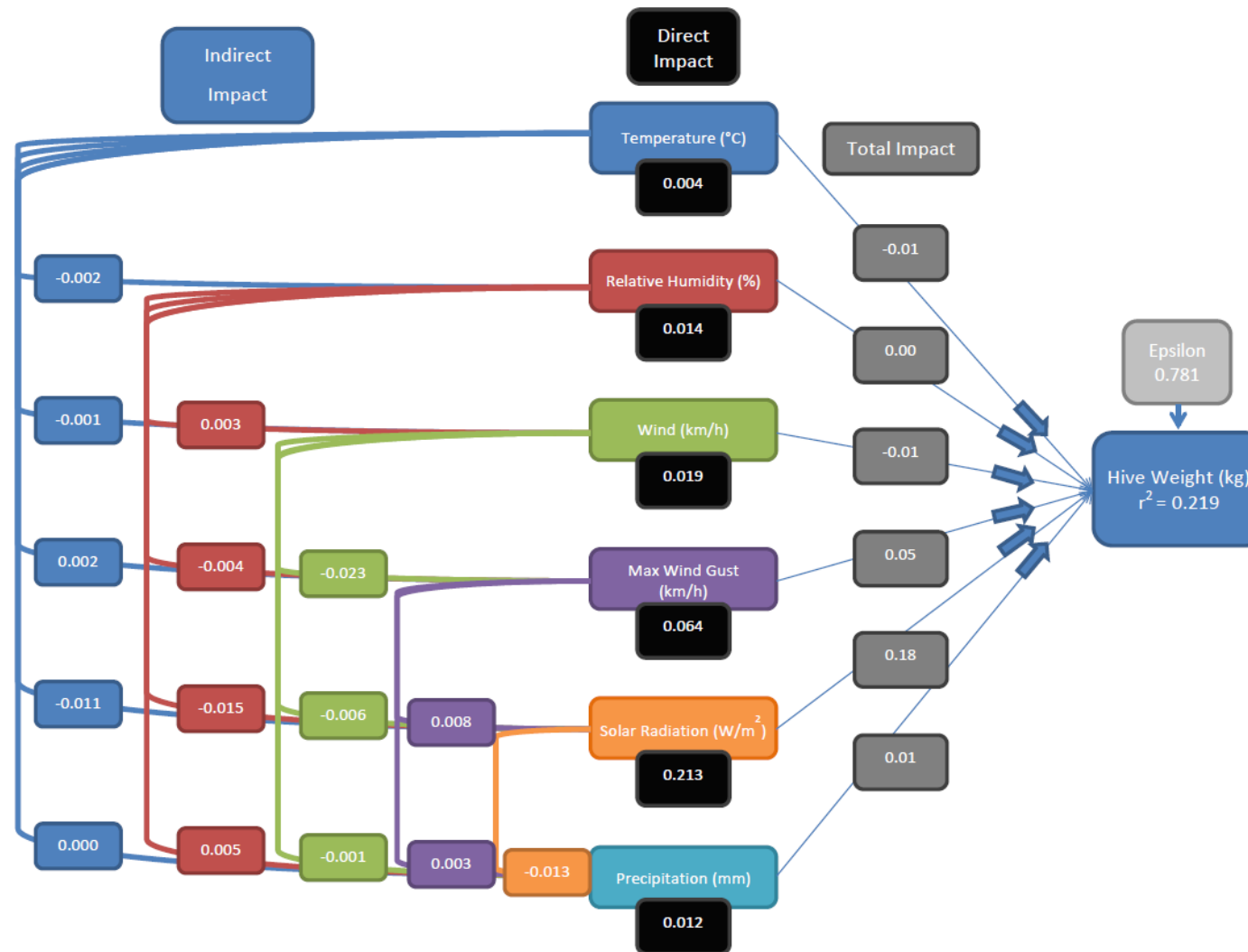


Figure 6 Diagram of the path analysis of weather variables on hive weight. Numbers on the left show the correlation influence a weather variable (same colour) has on the other variables (different colours). Total impact is derived from adding the direct and indirect impact. Epsilon is $1 - r^2$, the unaccounted influence on hive weight.

